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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 82, NO. 4, PP. 261–265 JULY, 1955

ISOLATION OF SEXUAL STRAINS OF PLACODERM DESMIDS

RICHARD C. STARR

The rarity of observed sexual reproduction in natural populations of placoderm desmids and the lack of success in inducing the sexual response in cultures have resulted in the neglect of this otherwise promising group of green algae as tools for genetic research (Lewin 1954). The writer (Starr 1954a) reported the isolation of heterothallic sexual strains of *Cosmarium botrytis* var. *subtumidum* Wittr. which have served as material for the first genetic investigations in the desmids (Starr 1954b). Subsequent attempts to isolate other sexual strains of desmids have met with success. It occurred to the writer, therefore, that a brief report on the methods involved might be of benefit to other workers interested in the cytotaxonomy and genetics of these algae. Sexual strains of the following species have been isolated by the writer: *Cosmarium botrytis* var. *subtumidum* Wittr. (heterothallic, Nos. 3 and 4), *Cosmarium botrytis* var. *mediolaeve* West (heterothallic, Nos. 200 and 201), *Cosmarium subcostatum* Nordst. var. (heterothallic, Nos. 100 and 101), and *Closterium parvulum* Naeg. (homothallic, No. 1).[1]

Natural populations of desmids seldom exhibit evidences of sexual reproduction, but in those instances where zygospores are found they often appear in such large numbers as to indicate that the sexual response had been effected through the rare combination of certain necessary environmental conditions. Early investigators (DeBary 1858, Klebahn 1891, Klebs 1896) did achieve some success in inducing sexual reproduction in natural populations by bringing them into the laboratory, but later investigators using unialgal or clonal cultures never were able to induce a sexual response by manipulating the environmental conditions. Random pairing of unialgal cultures has been attempted, but this has not proved effective in discovering sexual strains even in such algae as *Chlamydomonas*, in which sexual reproduction is not so rare as in the placoderm desmids (Lewin 1951).

The writer has achieved some success by approaching the problem from a different point of view. Attempts have been made to isolate sexual strains only from natural populations of desmids in which there was already some evidence of sexual reproduction, either as pairs of conjugating cells or as mature zygospores. Although the rarity of observed sexual reproduction in the placoderm desmids imposes a natural limit on this method, its success

[1] The writer is indebted to Professor G. W. Prescott of Michigan State College for the identification of these species.

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can hardly be overlooked in view of the total failure experienced by workers using other methods.

From a preliminary study of the environmental conditions under which the sexual strains of *Cosmarium botrytis* var. *subtumidum* yield the highest percentage of zygospores, information was gained which proved useful in the subsequent isolation of sexual strains of other desmids. Light, composition of the medium,[2] and carbon dioxide appear to act as factors limiting the sexual response in *C. botrytis* var. *subtumidum*. The sexual response is induced routinely in this species by mixing the heterothallic strains in a shallow 65 mm. watch glass which rests on a glass triangle in the bottom of a petri dish. Depleted medium from either culture of the sexual strains is used to dilute the inoculum. Fresh medium causes prolonged cell multiplication and so delays the reaction. In earlier trials using pyrex spot plates rather than watch glasses, it had been found that zygospores were formed only on the rim of the depression in the spot plate or on the surface of the medium. The same quantity of inoculum produced a larger percentage of zygospores when placed in shallow watch glasses, but, even then, zygospores were rarely formed in the center of the dish. The theory that sexual responses in some algae might be intimately connected with photosynthesis has been advanced by several workers (Lewin 1954, Sager and Granick 1954). Therefore, carbon dioxide was considered as a possible limiting factor in inducing zygospore formation in *Cosmarium botrytis* var. *subtumidum* in the deeper parts of spot plates or watch glasses. With this in mind, a 5% solution of sodium bicarbonate was substituted for the distilled water which had been added routinely to the petri dish in order to prevent excessive evaporation from the spot plate or watch glass. With this substitution zygospores are formed regularly in all areas of the watch glass. The removal of carbon dioxide from the surrounding atmosphere by using a 5% solution of sodium hydroxide resulted in the complete absence of the sexual response. When populations in which pairing of the conjugants had already been effected were placed in a CO_2-free atmosphere, the pairs dissociated; replacement of the solution of sodium hydroxide with sodium bicarbonate was followed by a return to the sexual condition indicating the importance of carbon dioxide.

[2] The medium used in culturing all the species described in this paper is soil-water medium of Pringsheim (1950). It is prepared in the following manner: A small pinch of powdered calcium carbonate is placed in the bottom of an 18×150 mm. test tube and covered with $\frac{1}{8}$ to $\frac{1}{4}$ inch of garden soil. This soil of medium humus content should not have been fertilized recently with commercial fertilizer. The tube is then filled $\frac{2}{3}$ full with glass-distilled water and plugged with a cotton stopper. The tube of medium is steamed (not autoclaved) for a period of one hour on two consecutive days. It should be noted that this soil-water medium containing calcium carbonate is useful only for those desmids which prefer an alkaline medium. For species from non-alkaline waters, a medium such as that compounded by Waris (1953) for *Micrasterias* will probably have to be used.

The covered petri dish containing the mixed sexual strains is exposed to a cycle of 18 hours of light and 6 hours of darkness using a bank of "warm-white" fluorescent tubes. In order to get a maximum sexual response, it is necessary that the dishes receive approximately 500 ft.-c. of light. Quantitative relations between the degree of illumination and the sexual response remain to be investigated. A temperature of 20–23° C. is maintained throughout. Under these conditions of light, temperature, medium, and carbon dioxide, zygospores of *Cosmarium botrytis* var. *subtumidum* are formed usually within two to four days, depending on the physiological condition of the cells used; cells from old cultures in which rapid multiplication is not occurring often undergo a cell division prior to pairing and thus delay the process. A more critical study of the environmental conditions in relation to the sexual response is planned.

Closterium parvulum (No. 1) was isolated from a natural population collected near Bloomington, Indiana; it contained a variety of species of *Closterium* and other desmids. Microscopic examination of the population revealed the presence of a few zygospores whose origin could be readily attributed to *Closterium parvulum,* for the empty cell walls of this species would be seen in the mucilaginous sheaths which are commonly secreted at the onset of the conjugation process (Starr 1954a). Although only a few vegetative cells of *C. parvulum* were observed in the collection, six individuals were isolated and placed singly in tubes of soil-water medium. After the cultures had become established, examination showed the presence of sexual stages in all the clonal cultures indicating that these strains of *Closterium parvulum* are homothallic.

The heterothallic strains of *Cosmarium subcostatum* (Nos. 100 and 101) and *Cosmarium botrytis* var. *mediolaeve* (Nos. 200 and 201) were isolated from a single natural collection sent to the writer by Professor Harold C. Bold of Vanderbilt University. On receipt of this collection, a microscopic examination showed the presence of a large number of zygospores formed by cells belonging to *Cosmarium subcostatum*. Pairs of conjugating cells could not be found but vegetative cells were present in great numbers. Although vegetative cells could have been isolated at random and later mixed in order to identify the compatible sexual strains, it would have simplified this identification if the members of a pair of conjugants could have been separated and used to produce clonal cultures. In an effort to secure such pairs, some of the crude material was mixed with the liquid supernatant of a soil-water tube and placed in a watch glass under the same conditions of light, temperature, medium, and carbon dioxide tension, described above for eliciting the sexual response in *Cosmarium botrytis* var. *subtumidum*. Within a few days, pairs of cells of *C. subcostatum* could be observed. Cells of *Cosmarium botrytis* var. *mediolaeve* were also observed

pairing, although no evidence of sexual reproduction of this species had been observed in the examination of the crude culture on arrival.

Pairs of both species were isolated singly into the depressions of pyrex spot plates containing soil-water medium. The dishes were then put in the dark until the following day; early experiments with *Cosmarium botrytis* var. *subtumidum* had shown that conjugating cells would usually dissociate if placed in the dark for as long as 24 hours. Separation of the conjugants by purely physical means is extremely difficult and often results in injury to one of the conjugants because of the layers of mucilage secreted at the beginning of the conjugation process. Following separation, each exconjugant of a pair was placed in a tube of soil-water medium. After sufficient multiplication had occurred, cells from each pair of cultures were tested for sexual behavior both singly and in combination by placing them under environmental conditions known to favor conjugation in *C. botrytis* var. *subtumidum*. In both *C. subcostatum* and *C. botrytis* var. *mediolaeve*, zygospores resulted only when cells of a culture arising from one exconjugant were mixed with those from its respective mate, indicating the heterothallic nature of the sexual response.

Zygospore formation in natural populations appears to coincide with those environmental situations which provide good illumination and rapid absorption of carbon dioxide from the air. Fritsch (1953) stated that the apparent special conditions necessary for inducing sexual reproduction in the desmids seem to be most often realized in small ponds or shallow pools. Workers with planktonic desmids rarely observe sexual stages in these species. Lund (Teiling, 1950, p. 316) reported that a five-year period of weekly examinations of the desmid plankton in Lake Windemere failed to produce a single zygospore. Teiling (1950) concluded that the degree of illumination was the limiting factor in this and similar situations. It is interesting to speculate that by placing natural populations of desmids under environmental conditions which have been found to elicit the sexual response in the species discussed in this paper, one could reasonably expect to discover sexual potentialities in other strains which would otherwise be overlooked. It should be remembered, however, that unless sexually-compatible strains are present in the natural population, no combination of environmental factors can be expected to induce the sexual response. There is always the possibility that mutations selected during years of multiplication by asexual means may have resulted in individuals incapable of sexual reproduction.

SUMMARY

1. Heterothallic sexual strains of *Cosmarium botrytis* var. *subtumidum* Wittr., *Cosmarium botrytis* var. *mediolaeve* West, and *Cosmarium subcostatum* Nordst. var. have now been isolated in clonal cultures.

2. A homothallic strain of *Closterium parvulum* Naeg. also has been isolated.

3. Methods used in isolating the cultures and in inducing sexual reproduction are described.

4. Light, carbon dioxide, and the composition of the medium are important environmental factors to be considered in inducing the sexual response in cultures of desmids.

5. It is suggested that these factors may also control the sexual response of desmids in nature.

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BLOOMINGTON, INDIANA

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THE SHOOT APEX AND LEAF OF DIANTHUS CARYOPHYLLUS L.

SAM SHUSHAN AND MARION A. JOHNSON

Histological investigations made on the shoot apex during the past two decades, while quite extensive (see reviews by Foster 1939, 1941; Philipson 1949, 1954; Johnson 1951 and Gifford 1954) indicate that further work is needed in this field. In the Caryophyllaceae Schnabel (1941) has explored the structure of the shoot apex including the origin of the leaf primordia and axillary bud meristems in *Honckenya peploides, Silene maritima* and *Dianthus caryophyllus*. The following observations extend our knowledge in this family as recorded here for *Dianthus caryophyllus* L.

Materials and methods. Lateral branches, 4 to 20 centimeters long, of the white flowering carnation, *Dianthus caryophyllus* L. (horticultural varieties Joan Marie and Maytime), were obtained from mature plants grown in gravel culture in a complete nutrient solution (Davidson 1946). The data on axillary buds include observations made on the varieties Maytime, Atlas, and Jupiter. All material was killed and fixed in formalin-acetic acid-alcohol (5 parts commercial formalin, 5 parts glacial acetic acid, and 90 parts of 50 per cent alcohol) and immediately aspirated for 30 minutes. Subsequently the tissue was dehydrated in a tertiary butyl alcohol series and infiltrated with tissuemat (M.P. 56–58 degrees centigrade). Sections were cut at 5, 7, and 10 microns in thickness and stained in anilin blue and safranin; fast green and safranin; Heidenhain's iron-alum hematoxylin and safranin; and Conant's quadruple stain (Johansen 1940).

General features of the shoot apex. The shoot apex of vegetative branches is dome-shaped in longitudinal section and elliptical in transverse section (figs. 1–6 and 12–19). Foliar buttresses arise from it in decussate succession. In the course of a plastochrone, the apex undergoes marked cyclical changes in volume. A maximum occurs immediately preceding the initiation of a pair of foliar buttresses (fig. 1). Following the initiation of the buttresses, the apex continues to contribute to foliar development and consequently decreases in volume until a minimum is reached (figs. 2, 3). Thereafter, the apex is gradually built up again until maximum volume is once more attained (figs. 4, 5, 6).

Measurements were made of the shoot apices of 50 lateral vegetative branches 4 or more centimeters long. The axils of the youngest pair of leaf primordia were used as points of reference for all measurements, except when only the foliar buttresses were present, in which case the adaxial sur-

face of the bulge was arbitrarily chosen as the base of the apex. The average dimensions obtained were: minor axis, 135 μ; major axis, 155 μ; and height, 63 μ. The largest apex had a minor axis which measured 162 μ, a major axis of 174 μ and a height of 93 μ; while the smallest apex had a minor axis of 85 μ, a major axis of 126 μ, and a height of 33 μ.

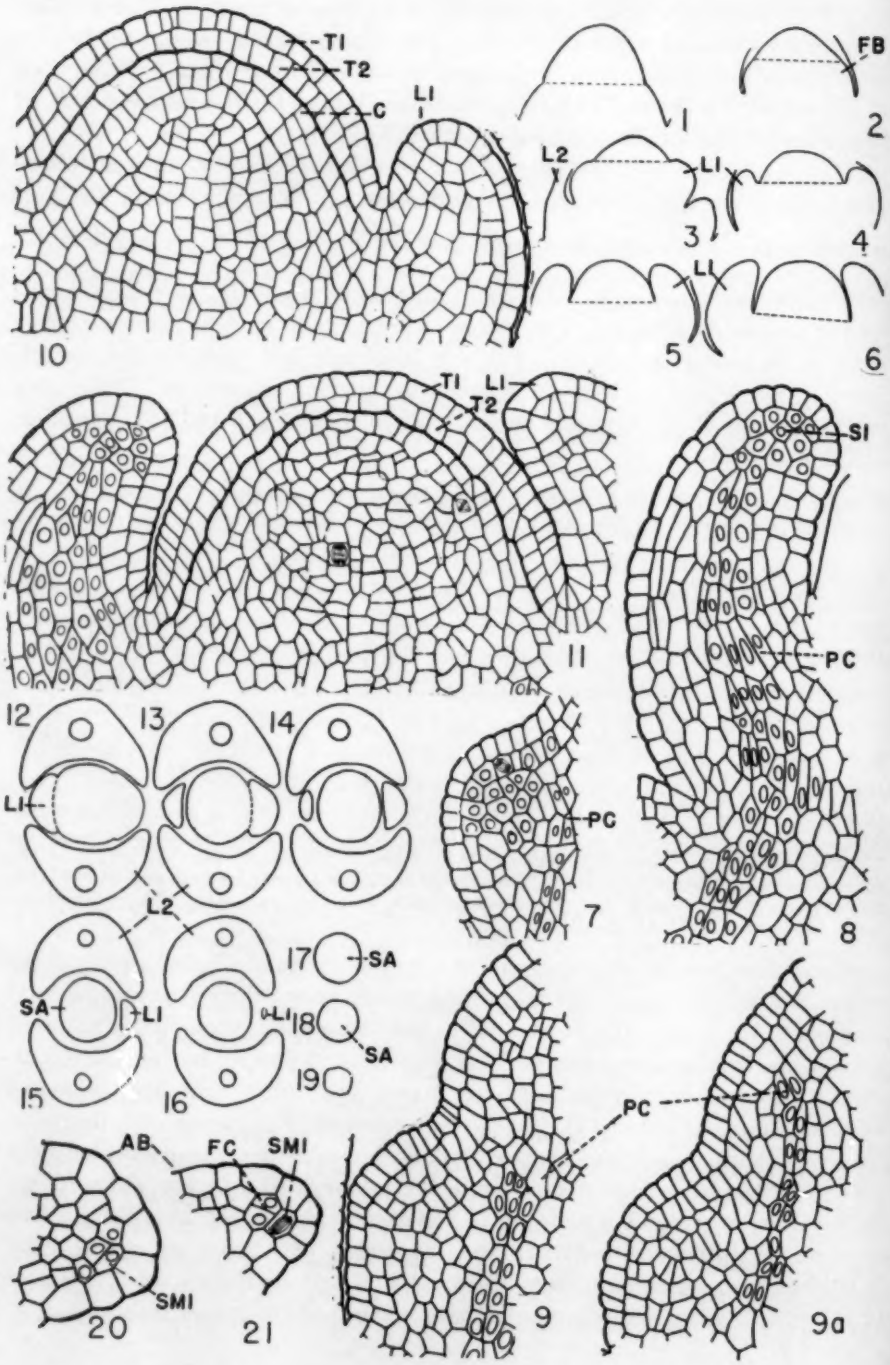
If it is assumed that the apex is half an ellipsoid (Ball 1941), the above measurements lend themselves to volumetric computation. Using the formula for the volume of half an ellipsoid, $\frac{4/3\pi(W/2)(L/2)H}{2}$, where "W" designates the minor axis, "L" the major axis, and "H" the height, the volume can be ascertained. The volume at maximum may be approximately seven times that at minimum (Table 1, shoot apices 1 and 3 respectively). There seems to be a correlation between the increase in volume of the apex and the height of the first and second pair of leaves, L-1 and L-2, as shown in Table 1.

TABLE 1. *Data on the shoot apex during a cycle*

Shoot Apex	Volume ($\times 10^5\mu^3$)	Height of L-1 (in microns)	Height of L-2 (in microns)	Dimensions of Apex		
				Minor Axis	Major Axis	Height
				(in microns)		
1	13.7	95	800	162	174	93
2	4.5	foliar buttress	240	126	150	45
3	1.9	foliar buttress	255	85	126	33
4	5.8	25	400	137	156	52
5	6.4	50	600	128	161	59
6	11.2	74	660	153	168	83

Note the general correlation between the volume of the shoot apex, the height of the youngest pair of leaves (L-1), and the height of the second youngest pair of leaves (L-2). Shoot apices 1–6 represent figures 1–6 respectively. (The apices used in this table terminated lateral branches 11–15 cm. in length.)

Concurrent with the cyclical change in volume of the apex, there occurs a reorientation of the major and minor axes. When the volume is at maximum, the major axis is parallel to the face of the youngest pair of leaf primordia. During the initiation and growth of the next pair of foliar buttresses and leaf primordia, both the major and minor axes are shortened and the minimum volume for the cycle is reached. Further growth increases the apical volume and lengthens both axes, but now the major axes is in the plane of the former minor axis while the minor axis is in the plane of the former major axis. This rotation of the major and minor axis through 90 degrees results momentarily in the formation of a circular apical base. When the apex has regained its elliptical base and maximum volume, a pair of foliar buttresses are produced at the expense of the major axis.


T1
T2
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L1
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L1
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17
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SA
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9
9a

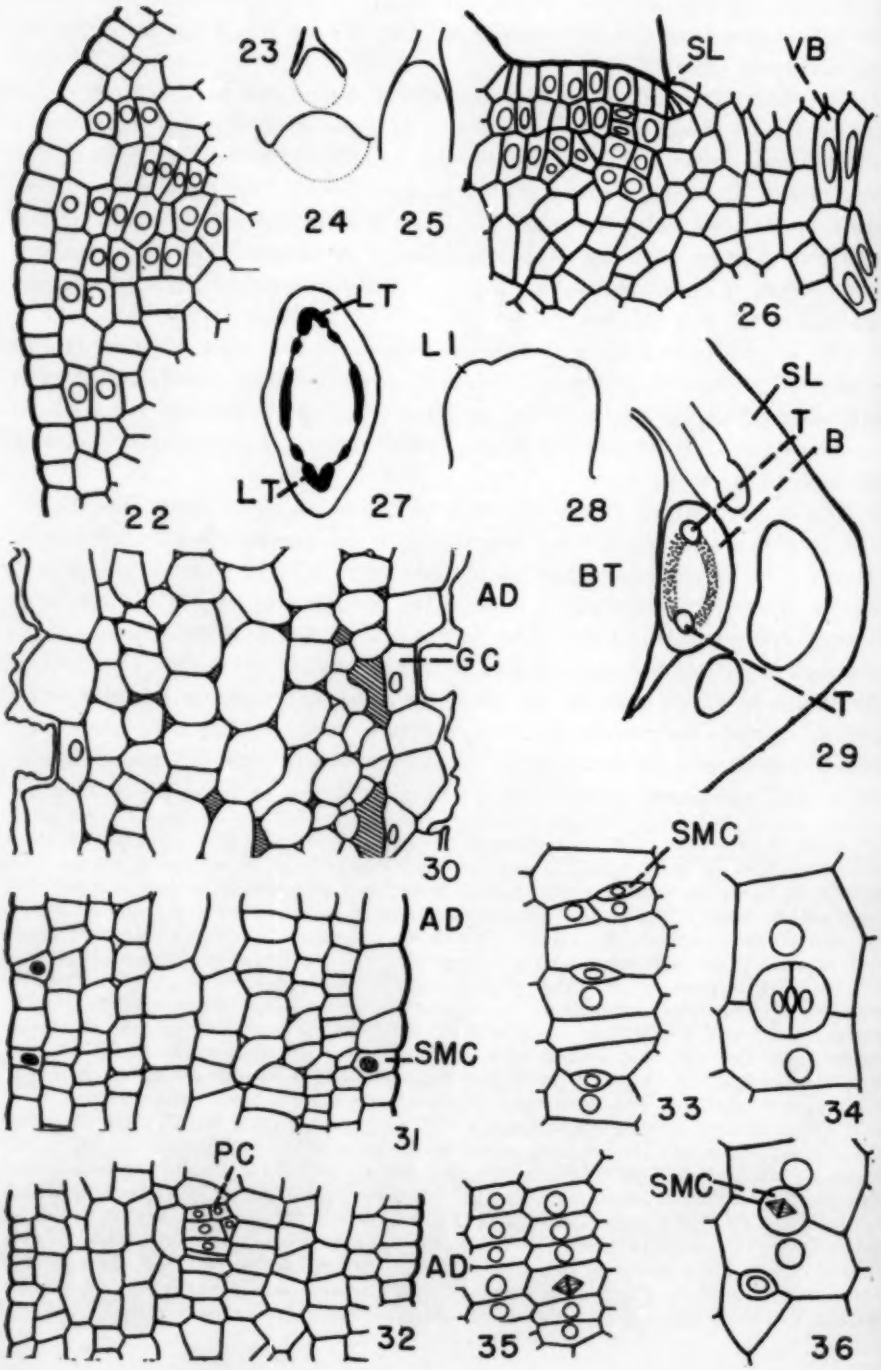
Tunica-Corpus of the vegetative apex. Topographically, the vegetative apex consists of a cuticle approximately 0.5 μ thick, a biseriate tunica, and a corpus (figs. 10, 11).

The outer layer of the tunica, henceforth designated as T-1, is approximately 7 μ in thickness. It is composed of genetically related cells which undergo only anticlinal division, thereby increasing the surface area of the shoot apex. These cells are destined to give rise to the epidermis of leaf and stem. Cytologically the cells of T-1 are thin-walled, nearly isodiametric, and have densely staining, "non-vacuolate" cytoplasm. The nucleus, containing one or occasionally two highly refractive nucleoli, occupies about one-half of the cell volume.

The second tunica layer, T-2, is centripetal to T-1 (figs. 10, 11). It also is about 7 μ thick and has thin-walled, approximately isodiametric cells with staining properties identical to those of T-1. Cell division is anticlinal except at the time of leaf initiation, when periclinal divisions occur near the base of the shoot apex.

The corpus, which forms the bulk of the shoot apex, underlies the biseriate tunica and, as in other angiosperms, is characterized by growth in volume. Cell divisions occur in all planes. There may be considerable stratification, however, in the outer part of the corpus (fig. 10). The first layer directly centripetal to T-2 will be referred to as C-1 and the second as C-2 although these are not discrete in the strict sense of the term. The cells of the corpus resemble those of the tunica in being approximately isodiametric and in having thin walls, dense cytoplasm, large nuclei and prominent nucleoli. Evidence for zonation in the corpus, based upon cell size, cell contents, wall thickness, or staining properties, seems to be entirely lacking.

FIGS. 1–21. FIGS. 1–6. Longisections through six shoot apices arranged to show volume changes of apex during a plastochrone. Figure 1 is at maximum volume and figure 3 at minimum volume. × 88. FIG. 7. Young leaf primordium in longisection; *PC*, procambium. × 266. FIG. 8. Leaf primordium in longisection showing procambial strand *PC*, and subapical initials, *SI*. × 367. FIGS. 9–9a. Drawings from two consecutive longitudinal sections through shoot apex showing early differentiation of procambial strand, *PC*, before leaf primordium which it is to supply has been elevated. × 367. FIG. 10. Shoot apex immediately after minimum volume has been attained; note stratification in corpus, *C*, *T1* and *T2*, tunica; *LI*, first leaf. × 377. FIG. 11. Shoot apex at maximum volume, note that the stratification seen in apex at near minimum volume (fig. 10) has been disrupted. × 377. FIGS. 12–19. Transections showing decussate arrangement of leaf primordia, *L1* and *L2*, and shoot apex, *SA*, near minimum volume, drawn at 6 μ intervals. × 40. FIG. 20. Transection through leaf showing submarginal initial, *SMI*, note that the original initial had divided tangentially to the edge of the leaf thereby adding a cell to the middle mesophyll and forming the new initial, *SMI; AB*, abaxial surface. × 367. FIG. 21. Transection through leaf showing the submarginal initial, *SMI*, adding a cell to the lower mesophyll, note that a cell, *FC*, to the left of the *SMI* has divided tangentially to the surface thereby doubling the original upper mesophyll layer. × 367. Legends; *FB*, foliar buttress; *L1*, first leaf primordium; *L2*, second leaf primordium; *SI*, subapical initials; *PC*, procambium; *T1* and *T2*, first and second tunica layers; *C*, corpus; *SA*, shoot apex; *SMI*, submarginal initials; and *AB*, abaxial surface of leaf.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The organization of the corpus varies with the stage in the plastochrone cycle at which the apex is observed. For example, the corpus of an apex at or near minimum volume is highly stratified and is composed of a relatively shallow cap, generally not more than 3 to 6 cells deep (fig. 10). The outer part is stratified into C-1, C-2, and occasionally C-3, while the inner cells are not arranged in a definite pattern. As the apex increases in volume, anticlinal, periclinal, and oblique divisions occur throughout the corpus, thereby disrupting the stratification noted at minimum volume (fig. 11).

Short files of rib meristem may appear in the base of the shoot apex above the first pair of leaf primordia. The best display, however, is seen in the internodes below.

The pith, vascular system, and most of the cortex of the axis are derived from the corpus. In the leaf, however, T-2 appears to make a greater contribution to the vascular tissue than does C-1.

Axillary branches. Axillary branches in the variety Joan Marie are arranged in four ranks with a single bud at each node. Since only one leaf axil of each pair of leaves bears a branch, it is obvious that branch arrangement cannot be described in terms of the $\frac{1}{2}$ phyllotaxis found in *Dianthus*. It would seem appropriate therefore to use the term cladotaxis here for indicating branch arrangement. Accordingly the variety Joan Marie possesses a $\frac{1}{4}$ cladotaxis which may be either clockwise or counter-clockwise. No exception to this arrangement was found in our material of this variety.

Histologically, the earliest indication of axillary bud formation can be found in association with the next to youngest pair of leaf primordia. This

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FIGS. 22–36. FIG. 22. Transection through stem at level of leaf axil showing early stage in axillary bud initiation as recognized by a slight bulge and cellular alignment resulting from periclinal divisions. ×533. FIG. 23. Young branch primordium cut longitudinally in plane perpendicular to parent stem. ×130. FIG. 24. Branch primordium corresponding to that in figure 23 but cut tangentially to parent axis. ×130. FIG. 25. Branch primordium in advance stage of development before leaf primordia have been initiated. ×130. FIG. 26. Longisection of young branch primordium in axil subtending leaf, *SL;* note periclinal division in second tunica layer; *VB*, edge of median vein of subtending leaf, *SL*. ×540. FIG. 27. Transection of stem below node, note that the vascular tissues are disposed roughly in four tracts; *LT*, leaf trace. ×18. FIG. 28. Longisection of branch primordium showing elevation of first pair of leaf primordia (prophylls), *L1*. ×130. FIG. 29. Transection through parent axis showing base of branch, *B*, and subtending leaf, *SL*, note two prominent branch traces, *T*, and stippled ares of procambium. ×72. FIGS. 30, 31, 32. Longisections taken 7 mm., 5 mm. and 0.3 mm. respectively from the base of a leaf 15 mm. long. Note that maturation is basipetal; *AD*, adaxial surface; *GC*, guard cell; *SMC*, stomatal mother cell; *PC*, procambium which will produce a transverse vein connecting the parallel veins of the leaf. ×370. FIGS. 33, 34, 35, 36. Longisections cut tangential to surface of a leaf 14 mm. long for stages in stomatal development. FIG. 35. Epidermal cells from near base of leaf, daughter cells are approximately equal in size. ×550. FIG. 33. Section taken 3000 μ above base of leaf, note that stomatal mother cells, *SMC*, have arisen from unequal division of epidermal cells. ×567. FIG. 36. Section cut 4000 μ above base of leaf.

is recognized by scattered periclinal divisions in the subsurface layers of the parent axis immediately above the leaf axil. In plants having a $\frac{1}{4}$ cladotaxis only one bud would develop at a given node and furthermore the axil in which bud growth would continue would be four nodes above the last bud produced in that rank. On the contrary bud growth in the opposite axil would not continue but the nearest bud in this rank would be two nodes below. This is precisely what happens and the position of the developing bud is soon marked by a small lateral bulge (figs. 22, 26). Growth in the opposite axil, beyond the initiating periclinal divisions, was not found in the variety Joan Marie.

Meristematic activity builds the familiar shell zone of flattened cells seen in the development of axillary buds. This zone, however, is not as distinct as that reported by Garrison for *Syringa* (1949a). Transections through the young bud show it to consist of a lenticular core of meristematic tissue flattened parallel to the surface of the parent axis and extending from immediately above the leaf gap into the slight bulge at the surface. This bulge (figs. 22 and 26) expands acropetally to become a mound-shaped branch primordium which is likewise flattened between the parent axis and the subtending leaf (figs. 23, 24, 25, and 29).

The first pair of foliar buttresses appear when the axillary branch primordium is about 100 μ high (fig. 28). They are always oriented at right angles to the subtending leaf and give rise to a pair of prophylls. Subsequent leaves are arranged in the usual decussate phyllotaxis.

The axillary shoot apex, during the course of a plastochrone, follows essentially the same developmental pattern described for the vegetative apex of branches 4 to 20 cm. in length. However, its volume increases until five to six plastochrones have been produced and the longest leaves are 4 cm. long.

Histologically, there is no discernible difference between young and older vegetative apices. A two-layered tunica is present in the early stages of axillary bud development long before the first foliar buttress is differentiated. The corpus, as in the older vegetative apex, shows no evidence of zonation; cell size, cell wall thickness, vacuolation, and staining properties are highly uniform throughout.

Difficulty was experienced in determining the precise course of procambialization. Branch and leaf gaps are continuous and only a few cells separate the procambium of the parent axis from the meristematic tissue of the axillary bud. Early in the development of the bud, two procambial strands bridge this short distance. They appear to differentiate acropetally and eventually become the midribs of the prophylls of the first node. Subsequently, these traces are incorporated into the cylinder of procambium of the branch axis (fig. 29 *t*).

The protophloem differentiates before the protoxylem. The direction of differentiation is acropetal from the phloem of the parent axis into the two branch traces and prophylls. The protoxylem differentiates bidirectionally, i.e. (a) basipetally from a center slightly below the first node of the branch into the branch traces until connection is made with the xylem of the parent axis, and (b) acropetally into the prophylls.

The vascular system of an axillary branch of the parent axis, as seen in transverse section, consists of four opposed arcs or tracts tied together by an active cambium and its derivatives (fig. 27). Each of the arcs represents the vascular supply of one of the ranks into which the leaves are disposed. Below each node the central part of the arc (fig. 27, *lt.*) 'separates' from the edges and 'passes upward' into the leaf. The edges of the arc continue distally as rather discrete bundles. They broaden tangentially and shortly unite, thereby closing the combined leaf and branch gap. The resulting broad, common stand passed up to the next node in the rank where it gives off another leaf trace. The vascular supply throughout the rank may be visualized as a trough-shaped tract with a series of centrally placed, superimposed gaps subtended by departing leaf traces. Thus, the leaves of a given rank are closely tied together. Likewise, the axillary buds, with their basal traces joined at the edge of the leaf gap, are in close contact with the vascular system of the parent axis. This may be of significance in determining bud arrangement.

There is considerable variation in axillary bud arrangement in the varieties of *Dianthus caryophyllus*. For instance, in the variety Maytime, from which a crop of flowers had been harvested, occasional branches developed in both leaf axils at the first node below the cut. In such instances, the larger bud occupied the expected position in the usual four ranked arrangement. Twenty strong branches of this variety were dissected for axillary buds of branch primordia, henceforth referred to as buds. In nineteen of these two buds were found at the first node counting upward from the base of the branch, but only one had two buds at the second node. Furthermore, three had two buds at the third node, one had two at the fourth and five had two at the fifth. Instances of two buds at a node above the fifth node were not observed. It should be emphasized that the buds at nodes 1, 3, and 5 lie in the ranks founded upon the first node of the branch and that in the twenty plants studied these nodes bore two buds more frequently than the nodes in the other two ranks. This is probably not without significance since the odd numbered nodes (1, 3, and 5 here) are in the ranks which were early connected through the branch traces with the vascular system of the parent axis. It was noted also that when a node bore two buds, one bud was generally larger than the other and the larger usually occupied the expected position in the $\frac{1}{4}$ cladotaxis. Occasionally, a branch

occurred at the expected node but not in the expected rank; rather, it was in the opposite rank and from that point on the cladotaxic spiral was reversed.

Another interesting variation was found in the variety Atlas, which produced two buds at several of the nodes below a flower. In one hundred and twenty-four plants examined, 87 per cent had two buds at the first node below the flower, 98 per cent had two at the second, 81 per cent had two at the third, and 30 per cent had two at the fourth. Below this level, the $\frac{1}{4}$ cladotaxis prevailed. However, in a comparable planting of the variety Jupiter, less than 3 per cent of the plants had two branches at the first, third, and fourth nodes below the flower while 10 per cent had two at the second node.

Mature leaf. The mature, grass-like carnation leaf ranges from 2–13 cm. in height, 3–7 mm. in width and approximately 400 μ in thickness, except at the midrib where it may be nearer 650 μ.

The blade consists of a heavily cutinized upper and lower epidermis, two upper and one to two lower palisade layers, and four to six layers of middle mesophyll traversed by parallel veins and numerous transverse or oblique connecting veins. Guard cells, present in both epidermal layers, are lacking in the adaxial surface near the base of the blade. Druse-containing idioblasts occur occasionally in the mesophyll of blade and sheath. The sheath is relatively less differentiated than the blade. Palisade cells are absent; intercellular spaces are small; and stomata are not found in the adaxial surface although they do occur in the epidermis of the stem which is closely enveloped by the sheath.

Origin and growth of the leaf primordium to 90 microns in height. When the apex approaches maximum volume it is generally possible to demonstrate the presence of two procambial strands extending from the procambium of the axis to C-2 or even C-1 towards the position of the next pair of foliar buttresses (figs. 9 and 9a). These are the traces to the next pair of putative leaf primordia and are considered here to be the first indication of leaf initiation. Shortly thereafter, periclinal and oblique divisions appear in T-2 and C-1 at both ends of the elliptical base of the shoot apex. Now the foliar buttresses, through lateral and acropetal expansion, are extended beyond the contour of the apex. This is correlated with an increase in anticlinal divisions in T-1 and with further periclinal and oblique divisions in T-2, C-1 and to some extent in C-2. Subsequently cellular stratification, parallel to the long axis of the shoot, is established within the foliar buttresses. Derivatives from a terminal group of initials in T-2, centrad to the foliar buttresses, together with intercalary growth elevate the leaf primordia (fig. 7).

Primordia 50 μ in height are crescent-shaped in transverse section while

at 90 μ they have become broadly trough-shaped and flexed in the direction of the shoot apex (fig. 8). Growth beyond this stage is largely in length and width. The primordia, exclusive of the procambial strands, are now some nine cells in thickness at the base and seven to eight cells in thickness at the midpoint. In view of the fact that the mature leaf is eleven to twelve cells in thickness, only two to four more divisions periclinal to the surface can be expected. Early contributions to length are made by a group of subapical initials (fig. 8, *si*) and by mitotic activity throughout the primordium; later, the major contribution in length is made by a conspicuous plate meristem. Increase in width is initiated by submarginal initials extending throughout the length of the primordium and is supplemented by derivatives from the plate meristem.

Foliar development beyond a height of 90 microns. The simple, entire, sessile carnation leaf offers few criteria for demarking stages in its development other than in height. Since height varies with the position of the leaf on the plant and is influenced by environment, it was thought best to describe foliar development beyond a height of 90 μ in terms of the contribution made by the subapical initials, the submarginal initials, and the plate meristem together with procambialization, vascularization and differentiation of the mesophyll and epidermis.

Subapical initials. These are established at the tip of the primordia as an active meristematic cap of cells by the time a height of 90 μ has been reached (fig. 8, *si*). Divisions are largely periclinal to the tip of the primordia. Meristematic activity is completed when a height of 2 mm. is approached.

Submarginal initials. These extend throughout the length of the primordia in both edges. Their activity can generally be recognized by the time the primordia are 50 μ in height. Divisions are periclinal, anticlinal, and oblique but could not be demonstrated to occur in any regular sequence. The edges of the leaf are extended by anticlinal and anticlinal-oblique divisions (to the surface) which add to the adaxial and abaxial layers of the mesophyll (fig. 21, *smi*) and by periclinal divisions (to the edge) which add to the middle mesophyll (fig. 20, *smi*). Usually the cells flanking the submarginal initials divide periclinally to the surface and thus increase the thickness of the mesophyll (fig. 21, *fc*). The adaxial subsurface layer shows more frequent periclinal divisions than the corresponding abaxial layer and hence makes a greater contribution to the mesophyll. Meristematic activity of the submarginal initials is completed in a progressive basipetal sequence.

Plate meristem. Growth attributable to a plate meristem was not observed until the primordia were 190 μ to 500 μ high. Divisions periclinal to the tip predominate so that the length of the mature leaf, depending upon its position on the plant, may be as much as 20 or more times the breadth.

With the completion of subapical activity in the 2 mm. leaf, there also occurs a cessation of submarginal and plate meristem activity in the apical region and as the leaf continues to elongate, these meristems are restricted to its basal portion. The basal leaves (prophylls) of a branch have generally completed basal growth when 1 cm. in length but the upper leaves may continue to show meristematic activity in the basal region when 4 or more centimeters in length.

Procambialization. The early differentiation of the procambial strand in the foliar buttress has been described in the section on the origin of the foliar primordia. In the second pair of primordia, especially if they have attained a height of from 500 μ to 700 μ, two prominent lateral procambial strands are differentiated acropetally into the leaf apex and basipetally into the leaf base where they end blindly in the plate meristem. An occasional transverse strand, which has differentiated from the middle mesophyll, connects the laterals with the central strand. In the third pair of leaves, when approximately 2 mm. high, the two lateral procambial strands differentiate obliquely toward and finally join the central strand. Adult leaves generally have as many as 32 additional lateral veins with frequent transverse connecting strands. The pattern of procambial differentiation in these may be either bidirectional or basipetal.

Vascularization. In general, the first elements of the protophloem are differentiated in the second pair of leaves. Critical examination of 15 shoots showed this to be true in 12 cases, in the other three no sign of protophloem differentiation was evident in the second pair of leaves. The direction of differentiation is acropetal from mature phloem below. This may be illustrated by two examples. In one instance a group of sieve tubes was found on each side of the leaf gap of a 3 mm. leaf situated directly beneath a leaf primordium 150 μ in height. From each of these groups a sieve tube had differentiated acropetally for a distance of 40 μ toward the 150 μ leaf primordium. In the second instance, sieve elements had differentiated 80 μ from a similar position toward a 270 μ primordium when a break occurred. Above this break, sieve elements continued for 150 μ into the primordium.

The critical stage for protoxylem differentiation is to be sought in the traces to the third pair of leaves. In 29 of 30 branches examined, lignification was clearly evident in the third pair of leaves but in no instance was it found in the second pair. Once protoxylem differentiation is initiated it spreads rapidly throughout the trace so that difficulty is experienced in locating the precise point of origin. There is, however, sufficient evidence to indicate that differentiation is generally bidirectional from a center near the base of the leaf. For example, it can usually be demonstrated that there are a few more lignified elements at or immediately below the level where the leaf is attached to the stem than at other levels in the trace. Further-

more it was possible to follow the protoxylem of the trace to the third leaf into the third internode where it ended blindly. In slightly older leaves mature protoxylem of the leaf trace and of the axis were continuous. In the leaf proper, instances of basipetal protoxylem differentiation were found in the lateral veins. Veins connecting two lateral veins frequently showed the maturation of the xylem progressing toward each vein.

Mesophyll. The mesophyll is derived from the plate meristem and the submarginal initials. The overall pattern of cellular differentiation and maturation is basipetal. This is readily demonstrated in mature leaves about 1.5 cm. in length where the basal region is completely meristematic (fig. 32). Midway up these leaves the cells are noticeably larger, stomatal mother cells have differentiated, and there are numerous small intercellular spaces (fig. 31). In the distal portion, the intercellular spaces have increased in size, the stomatal units are nearly mature (fig. 30), and the differentiation of the palisade cells will soon be evident. Among the last cell types to undergo differentiation and maturation are bands of vein-associated fibers, one to three cells in depth. In transverse section these are seen in the form of a U-shaped band below the phloem of the midvein and about 10 cells removed from the sieve elements. They also differentiate in the form of a flat or arched band beneath the two main lateral veins and one or two of the other more prominent laterals. Differentiation is bidirectional and is to be sought above the middle of leaves about 1 cm. in length.

Druse-containing cells are found in the mesophyll. They occur in greatest concentration immediately adjacent to and below the fibers.

Mitotic figures were scarce in our material and it was difficult to ascertain the precise pattern in which cell division was completed. On the basis of indirect evidence, the epidermis appeared to be the first to cease division, followed in turn by the spongy mesophyll and finally by the palisade mesophyll. A rather constant exception to this sequence was found in the spongy mesophyll where divisions giving rise to interveinal procambium continued to maturity of the leaf.

Epidermis. The epidermis remains uniseriate throughout the ontogeny of the leaf; its cells divide either in a plane at right angles to, or parallel to, the long axis of the leaf. These divisions normally result in daughter cells of equal size (fig. 35). While the epidermal cells are apparently the first to stop dividing, they are the last to cease elongating. Maturation is basipetal.

The carnation is very favorable for demonstrating stages in stomatal development. The onset of stomatal initiation is marked by the appearance of unequal divisions in the epidermal cells near the tips of young leaves ranging from 650 to 1300 μ in height and may be observed in the basal portion (650 to 1300 μ) of larger but still immature leaves. This unequal divi-

sion is in a plane at right angles to the long axis of the leaf and results in a small, lenticular, distal stomatal mother-cell and a larger basal cell (fig. 33). The stomatal mother-cell increases in size and becomes spherical to elipsoidal in shape (fig. 36). Division in a plane parallel to the long axis of the leaf produces the immature guard cells (figs. 34, 36). This stage occurred near the apex of leaves 2000 to 4000 μ high or above the base (2000 to 4000 μ) of taller leaves. In three instances, a deviation from the normal pattern of guard cell formation was observed, when one of the guard cells divided transversely forming a stomatal unit consisting of a normal guard cell and two "half-sized" guard cells.

Discussion. Histological research on the angiospermous shoot apex has produced a voluminous literature much of which has been reviewed by Foster (1939, 1941), Philipson (1949, 1954), Popham (1951), and Gifford (1954). It is evident that a more uniform concept as to what constitutes the shoot apex would be helpful in providing comparable data as to shape, dimensions, and zonal patterns. Restricting the apex to the free part above the youngest leaf primordium accomplishes this except in more or less flat-topped apices where much of the surface is involved in the production of leaf primordia. These are difficult to fit into any scheme for comparable measurements since the corpus may actually lie below the axil of the youngest leaf primordium and the "sunken apex" must be delimited by such criteria as cell enlargement, vacuolation, mitotic activity, and differential staining.

Popham (1951) has wisely stressed similarity in apical structure throughout vascular plants. According to his classification *Dianthus caryophyllus* would be included in Type VII, the usual angiospermous type. There is no histological evidence in the material examined in this study for zoning the apex of *Dianthus* into mantle, subapical initials, central meristem and peripheral meristem as proposed for Type VII. Accordingly we have chosen to use the tunica-corpus concept in our descriptions. Admittedly many instances are now on record where real difficulty is experienced in distinguishing between tunica and corpus (Reeve 1948, Gifford 1950, and Popham and Chan 1950). Even so, the concept of growth in area as contrasted with growth in volume has been and still is extremely useful.

Surely it is recognized by this time that shoot apices have a central initiating core, composed of surface and sub-surface initials, of varying depth from which the primary tissues are ultimately derived. When histological differences warrant the separation of the initiating core and its derivatives into zones, the overall pattern of growth can still be profitably described in terms of growth in area vs. growth in volume. Some apices requiring this treatment are *Liriodendron* (Millington and Gunckel 1950); certain members of the Rosaceae (Rouffa and Gunckel 1951) and of the

woody Ranales (Gifford 1950); *Chrysanthemum morifolium* (Popham and Chan 1950); *Laurus nobilis* (Kasapligil 1951); several species reviewed by Philipson (1949), and others described by Majumdar (1942) and Mitra and Majumdar (1952). Apparently much exploratory work must be done before the full range of apical structure in the angiosperms can be appreciated and typed.

The impression is gained from the literature that, especially in opposite leaved plants, the change from maximum to minimum area (volume) of an apex is very abrupt and coincides with the time at which the foliar buttresses or leaf primordia can first be recognized. The apex in *Dianthus,* however, continues to contribute to the foliar buttresses after they become distinct, thus the change from maximum to minimum volume is a gradual one. It would be of interest to know whether this occurs in other opposite leaved plants. In *Dianthus caryophyllus,* and probably in most spermatophytes, the most reliable comparisons and correlations result from comparing growth stages of the apex or of young leaves with the volume instead of the basal area of the apex. Once the volumetric pattern is known for a species, volume of the apex becomes extremely useful as a tool in comparative studies. Care should be exercised in distinguishing between volume of the apex and that of one or more foliar buttresses often included in such comparisons. Schnaubel for example (1941), in a careful study on *Dianthus caryophyllus* and three other genera, has presented measurements and graphs showing that the height and width of the "Vegetationspunkt" increases during two plastochrons. Actually the apex has passed through two cycles of volume change which are masked in his measurements because they include the increase in breadth of the third node and height of the axis during the two plastochrons.

The perplexing problem of whether the foliar procambial strand is differentiated before or after the initiation of the leaf primordium has been discussed by Ball (1949). In *Lupinus* (Ball 1949) the leaf primordium is elevated and then the procambium differentiates basipetally into the axis. Conversely, in the carnation the median procambial strand is differentiated before the primordium which it is to supply is recognizable. This early differentiation of procambium is being reported for an increasing number of plants (Sterling 1945, Gunckel and Wetmore 1946, Esau 1953). No evidence was found in *Dianthus* in support of basipetal procambial development which Ball believes is of more frequent occurrence than is generally realized. Our figures 9 and 9a suggest that procambial differentiation may have been acropetal, but the strands are too far advanced for conclusive proof. Once procambialization is instituted, it proceeds so rapidly that difficulty is experienced in obtaining material showing definite stages in support of either acropetal or basipetal differentiation.

The adaxial meristem, which plays a prominent role in the development of the petiole and midrib in many leaves, is lacking in *Dianthus* (Avery 1933, Foster 1935).

The strongly developed plate meristem contributing primarily to the length of the leaf, and the wave of maturation which sweeps down from the tip of the leaf, is reminiscent of grasses (Sharman 1942). In fact, the plate meristem in carnation may well be thought of as a basal or intercalary meristem, as it is frequently designated in grasses.

Modern studies in the development of the shoot show that an extremely close relationship exists between the foliar buttresses and the axis. They also point up the difficulties involved in attempting to isolate leaf and axis as discrete units. This is readily seen to be the case in *Dianthus* where two or three pairs of foliar buttresses are produced in rapid succession without evident internodes. Later, growth at the base of the foliar buttresses gives rise to the internode. Mitra and Majumdar (1952), report a similar condition in 14 species of dicotyledons and believe that the shoot axis is composed of an axial core surrounded by a mantle of leaf bases. The mantle-core theory has appeared in the literature under various guises (Hofmeister 1851, Potonie 1902, Saunders 1922). Of the problems which have beset this theory, one has been the radial delimitation of the mantle. Mitra and Majumdar would solve this difficulty by the recognition of two histogens in the apex. They report that in some of the dicotyledons which they have studied there is evident zonation as follows: "a zone each of the central mother initials, the flank meristem and the file meristem (the last is derived exclusively from the corpus cells)." The file and flank meristems arise from the central mother initials. The flank meristem, in turn, produces the mantle and the file meristem initiates axial core or pith. Thus, according to these authors "the radial extent of the mantle appears to extend up to the pith as suggested by Hofmeister." Histogen theories, when applied to the shoot apex have fared badly because of the irregularity of cell lineage or lack of discreteness in the required zonation. We, therefore, question the wisdom of determining the radial extent of the mantle on the basis of origin from the apex. Perhaps, morphologists should heed the sage advice of Agnes Arber (1930) who states in concluding a discussion on this problem: "If we once accept the fact that 'stem' and 'leaf' are no more than convenient terms, which should not be placed in antithesis as if they corresponded to sharply opposed morphological categories, the problems of their delimitation and of their differentiating characters vanish into thin air."

The origin and development of axillary buds in the angiosperms are apparently in need of further critical study (Garrison 1949a, 1949b and Gifford 1951). The principal problems center about the degree of isolation

of the bud meristem from the shoot apex and procambium of the parent axis and also the direction of procambialization between bud and parent axis. Our observations on *Dianthus* contribute little to either of these problems other than to emphasize the difficulty of their solution. Procambialization appears to be acropetal from the parent axis into the axillary bud. However, it was impossible to demonstrate the presence of meristematic traces which could be considered as the forerunners of the procambium as have been described in *Syringa, Betula* and *Euptelea* (Garrison 1949a, 1949b).

It is of interest, to note in *Dianthus,* that while the leaves are decussate, the buds tend to be arranged in a $\frac{1}{4}$ cladotaxis. The question immediately arises as to why a bud is not developed in each leaf axil as has been described for *Phlox* by Miller and Wetmore (1946) and for *Syringa* by Garrison (1949a). Physiological conditions must be favorable for the development of buds in both leaf axils of a node in *Phlox* and *Syringa* but apparently such is not generally the case in *Dianthus.* Can it be that a developing bud diverts essential metabolites to such an extent that they are no longer in sufficient supply for the development of a bud in the leaf axil immediately above? The $\frac{1}{4}$ cladotaxis would suggest that this might be a possibility. Also, when two buds develop at two consecutive nodes a strong bud develops above a weak one and conversely a weak bud occurs above a strong one.

This hypothesis might be tested further by determining the number of buds at the first node of a branch. Since the first node is early attached to the parent axis by two traces, we might expect a bud in both leaf axils. Not only does this frequently occur, but occasionally two buds were found at nodes 3 and 5 which are intimately connected with the traces of the first node. If this reasoning is correct the rarity of buds in both axils of the second node becomes significant in view of the fact that this node is not connected so early or so directly to the parent axis. These observations would suggest that existing buds may have a role in determining the size of subsequent buds and likewise the pattern of bud arrangement. The reversal of bud arrangement from clockwise to counterclockwise can hardly be explained by this hypothesis, for then a strong bud develops immediately above an equally strong bud. Likewise, the production of a bud in each axil for several nodes below a flower bud in the variety, Jupiter, requires explanation. The variation in bud arrangement in *Dianthus* merits further study. It is hoped that experimental studies will throw light on some of the problems raised in this account.

SUMMARY

1. The dome-shaped shoot apex of *Dianthus caryophyllus* L. consists of a two-layered tunica and a corpus. The outer portion of the corpus shows

considerable stratification especially when the apex is at minimum volume. No other zonation is apparent.

2. During a plastochrone the apex passes from a maximum, gradually to a minimum and back to a maximum volume.

3. Procambium can be traced to the base of a putative leaf primordium.

4. Apical growth in the leaf ceases by the time a height of 2 mm. is reached.

5. Submarginal activity begins when the leaf is approximately 90 μ high. Plate meristem activity begins when the leaf is about 190 μ high and during the basal maturation of the tissues is confined to the leaf base much as the basal meristem of grass leaves.

6. Stomatal development is described. There are no accessory cells.

7. Initial phloem differentiation is acropetal; differentiation of the first xylem elements in a midtrace is bidirectional from near the base of the third leaf. Subsequent maturation of vascular elements is bidirectional or basipetal. Two phloem strands differentiate toward a given leaf. These outline the leaf-branch gap of the leaf two plastochrons below before converging into a single strand which enters the leaf.

8. Axillary buds are arranged in a $\frac{1}{4}$ cladotaxis, their initiation and development is described. An hypothesis is suggested which may help in accounting for their arrangement.

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A SPECIES OF GRASS WITH LIQUID ENDOSPERM

WALTER V. BROWN

At maturity the grain or caryopsis of almost all species of grass loses water and becomes dry and hard. The embryo, seed coats, and endosperm lose water until they reach an equilibrium with their particular environment which, under conditions of dry storage, is about five to ten per cent of free moisture. In such a hard, dry condition the seeds of most grasses will remain viable, under the best storage conditions, up to about 20 years. The endosperm in such grains is cellular with the cells packed with starch grains or, in some cases, sugars or dextrin. There is some question whether such endosperm cells are alive or dead; most evidence indicates that they are dead.

A unique endosperm condition was recently found in the monotypic winter annual grass *Limnodea arkansana* (Nutt.) L. H. Dewey of south-central United States. When grains of this species, collected in May 1954, near Austin, Texas, were examined seven months later they were found to have liquid endosperm. The "seed coats" form a tough, pliable sac full, but not to turgidity, of liquid. Normally, the grain is enclosed in and remains within the spikelet structures until germination. The very hard glumes and the lemma protect the grain during this period of dormancy. The caryopsis itself is about 2 mm. long and weighs about one-third of a milligram.

When the tough "seed coat" is punctured or burst by pressure the thick, whitish endosperm extrudes. When put in water the endosperm becomes more solid, more opaque, and whiter. It is almost impossible to stir it into a homogeneous mixture, rather, it breaks up into small pieces like bits of cheese. There are two sizes of solid inclusions in the liquid, very small ones and much larger ones. Actually, the large ones are compound grains made up of the smaller type, but many of the small type are not incorporated into large compound grains. Under the polarizing microscope the grains do not give the typical cross pattern of birefringence produced by ordinary starch grains (wheat starch and rice starch). Treatment with 0.01 M iodine in .5 per cent potassium iodide solution changes these grains first to a reddish (magenta) color which later changes to violet or purple. This is similar to the reactions of rice and wheat starch when treated with this concentration of iodine. It is, therefore, assumed that these grains are composed of starch. Oil droplets of varying sizes are abundant. Since nitric acid turns it a pale yellow there is, apparently, some protein in this endo-

sperm. No cell walls nor remnants of walls were observed. Nuclei also were not seen when treated with acetocarmin, indicating that this endosperm is quite dead.

Caryopses from an herbarium specimen collected in 1939 and, therefore, having been under hot, dry herbarium conditions for 15 years, still had liquid endosperm, and the grains appeared no different from the seven-months old grains originally examined. Grains about 50 years old (1902 and 1913 collections) had a thick, pasty endosperm of cheesy consistency, and the caryopses were somewhat flattened. These specimens are on deposit in the herbarium of the University of Texas.

It is difficult to determine the relative importance of the "seed coats" as opposed to the osmotic factors of the endosperm itself in maintaining the liquid condition during very dry storage for many years. It is more than likely that both play a part. That the endosperm itself holds its water very firmly was evident when 31 caryopses weighing 10.0 mg. were broken open and the endosperm forced out into a tiny weighing dish. This was weighed again and placed in an oven at 70° C. In 24 hours, 0.3 mg. of water was lost, in three days 2.3 mg., and in five days constant weight was reached with 2.6 mg. of water lost. Even after three days the endosperm was still liquid. After five days the endosperm-covered seed coats were brittle and all extruded endosperm was dry. The seed coat itself permits the entrance of water, and germination takes place in a few days. The indicated water content of this endosperm is about 26 per cent, rather high for mature grains in dry storage. Since water leaves the endosperm with such difficulty, since the endosperm becomes white and opaque when put into water, and since it evidently contains protein, it is probable that this endosperm is colloidal in nature with included starch grains and oil droplets.

As far as known, this is the only recorded species of grass with liquid endosperm. It is apparent that this condition has not been observed, or at least published, previously in this species. Miss Agnes Chase of the United States National Museum checked taxonomic treatments of the species and failed to find any reference to it. The observation was new to her personally. I thank her for her valuable help.

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A TECHNIQUE FOR OBTAINING POLISHED SURFACES OF SECTIONS OF PYRITIZED PLANT FOSSILS

Charles B. Beck[1]

Many plant fossils have been preserved as compressions. From such specimens much valuable information has been obtained, most of which pertains to external form. Frequently, however, small portions of the axes of compression fossils are found which have been structurally preserved by infiltration of iron disulphide (FeS_2), commonly known as pyrite.[2] Specimens thus preserved, which allow a study of both external form and internal structure, are of considerably greater value to the morphologist than those in which external form or internal structure alone can be studied. With both areas of information available, one can determine the taxonomic relationships of a plant with considerably greater ease and accuracy.

Since pyrite is opaque, to study a pyritized fossil one must examine polished surfaces with reflected light. Great difficulty is usually encountered in obtaining a polished surface of such a specimen because of the tendency for cut surfaces to crumble when grinding and polishing are attempted. This tendency is increased when a large amount of carbonaceous wall material is present. Furthermore, pyrite oxidizes rapidly when exposed to the atmosphere, adding to the tendency to crumble. Because of these difficulties only a few workers have studied pyritized portions of axes in fossils primarily of a compression type.

Banks (1944) demonstrated internal structure associated with compressions of the Devonian lycopod, *Colpodexylon*. The writer has been engaged in such a study and has been able to demonstrate excellent structural preservation in pyritized axes of compression material of another interesting Devonian plant. This work will be published subsequently. The most outstanding example of work in which internal structure was studied in a compression fossil, and which best illustrates the value of such a study, is that of Leclercq (1951). Leclercq was able to clarify the previously rather vaguely defined genus, *Rachophyton*, and showed conclusively that *Racho-*

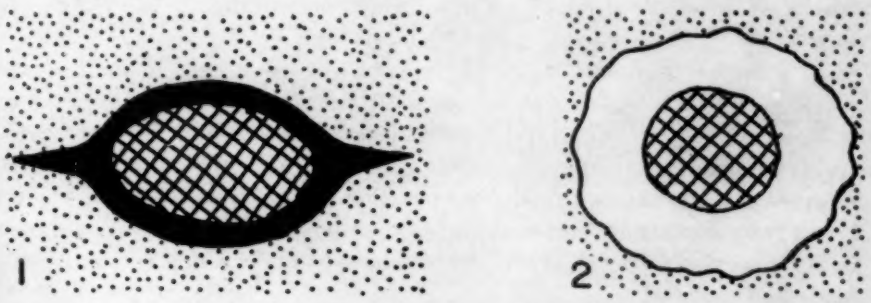
[1] The writer wishes to express his appreciation to Prof. H. P. Banks for aid in the preparation of the manuscript.

[2] The orthorhombic form of FeS_2 is commonly called marcasite. It is usually difficult to distinguish with certainty from pyrite, the cubic form. However, marcasite is said to have a tin-white color and pyrite is assumed usually to be brass-yellow. There seems to be no useful reason for distinguishing between the two forms of FeS_2 in this paper. The application of the technique to be described is identical for both forms. Therefore, the term, pyrite, will be used hereafter in this paper to include, when necessary, both forms of FeS_2.

phyton is a zygopterid fern. Without a knowledge of the anatomy of this plant the conclusion that it is a coenopterid would have been less certain.

The writer in studying pyritized axes of compressions has used a technique which greatly facilitates the study of these axes. This technique is useful not only in studying pyritized axes in compression fossils, but also in studying fossils preserved in any other manner in pyrite, where there is a tendency for a cut surface of the specimen to crumble when polishing is attempted.

Much fossil plant material structurally preserved by iron pyrite can be conveniently separated into two categories: That directly associated with compression specimens and that completely isolated from any specimen showing external morphology. Pyritized axes associated with compressions, as might be expected, usually show evidence of some compression and are oval-shaped in cross-sectional outline. The outer tissues seem usually to have been destroyed before or during preservation. Surrounding or partly surrounding the preserved portion of the axis there is, in many cases, a thin layer of dark, apparently carbonaceous material which probably consists of the decayed and compressed outer tissues. The cell walls of the preserved tissues, especially the xylem and sclerenchyma are generally composed of carbonaceous material with pyrite filling the lumina of the cells. Because of the abundance of carbonaceous wall material present and the discontinuity of the pyrite, there is a great tendency for cut surfaces of such specimens to crumble when polishing is attempted. The type of specimen described above is illustrated by figures 1, 5 and 6. Figures 5 and 6



FIGS. 1–2. Schematic drawings of two common types of fossil plants structurally preserved by pyrite. FIG. 1. This represents the type associated with compression specimens. The stippled area represents rock matrix; the black area represents the disintegrated and compressed outer tissues of the plant; the cross-hatched area represents the pyritized, structurally preserved portion of the plant. FIGS. 5 and 6 are photographs of this type. FIG. 2. This represents the type preserved within a mass of pyrite, usually not associated with a compression. The stippled area represents rock matrix; the white area, pyrite; the cross-hatched area, the region of cellular preservation. FIG. 4 is a photograph of this type.

are photographs of transverse sections made from small portions of pyritized axes taken from a compression specimen like the one in figure 3.

Isolated fragments of axes, unassociated with compression specimens, occur commonly. Such specimens may differ from the above described type by being completely embedded within a mass of pyrite. Such specimens may be found in pyrite nodules or concretionary masses, or in more or less continuous beds of pyrite such as the "Tully pyrite," the Leicester member of the Moscow formation, of the Middle Devonian in western New York. Plant parts embedded in such masses of pyrite may or may not be compressed. Quite frequently all tissues are preserved. Furthermore, in some cases, the organic wall material seems to have been nearly completely replaced and anatomical structure is indicated only by a discoloration of the continuous mass of pyrite. In such cases, little or no difficulty is encountered in the process of polishing cut surfaces. When, however, the carbonaceous wall material is not replaced by pyrite, crumbling of surfaces will occur. This type of specimen is illustrated by figures 2 and 4.

The value of studying the structurally preserved portions of axes of compressions has been indicated by the works cited above. Valuable contributions have also been made as a result of the study of isolated pyritized axes. Several new genera have been described from the "Tully pyrite" including *Iridopteris, Xenocladia* (Arnold 1940), *Schizopodium* and *Arachnoxylon* (Read 1938). *Aneurophyton* was first positively identified in this country by Arnold (1940) primarily on the basis of isolated petrified fragments found in the "Tully pyrite" and in marcasite nodules in the Marcellus formation in western New York. The new genus, *Reimania,* was also described from specimens found in marcasite nodules in the Marcellus (Arnold 1935).

A technique to aid in the preparation of pyritized plant fossils for study was described by Leclercq and Discry (1950). This technique involves embedding the fossil material in Canada balsam. The embedding process which involves immersion of the specimens in xylol for 12 hours, in a xylol-balsam mixture for 3 hours and finally evaporation of the xylol, requires 18 or 19 hours for completion. This technique is supposed to harden the specimens by a "progressive penetration" by the balsam after which sections can be made and polished.

The writer in applying this technique found that there was little or no penetration of the specimens by the balsam and that only the surfaces actually covered by balsam could be ground and polished with any success. The embedding medium, therefore, acts primarily to fill the depressions in the cut surface caused by the action of the saw blade and oxidation of the pyrite, and thereby, prevents a further crumbling of the surface when it is ground and polished.

After continued modification of this technique over a two year period, the writer recommends the following new procedure:

(1) Cut thin sections of the specimen. If the fossil is completely embedded in a rock matrix which is unfractured, no treatment is necessary prior to cutting. However, if the surrounding rock is friable, or already fractured, or if a considerable portion of the fossil material is exposed, the entire specimen should be embedded before cutting.

(2) Place the sections in a solution of 3 parts toluene and 1 part Harleco Synthetic Resin (HSR). Boil gently on a hot plate until most of the toluene

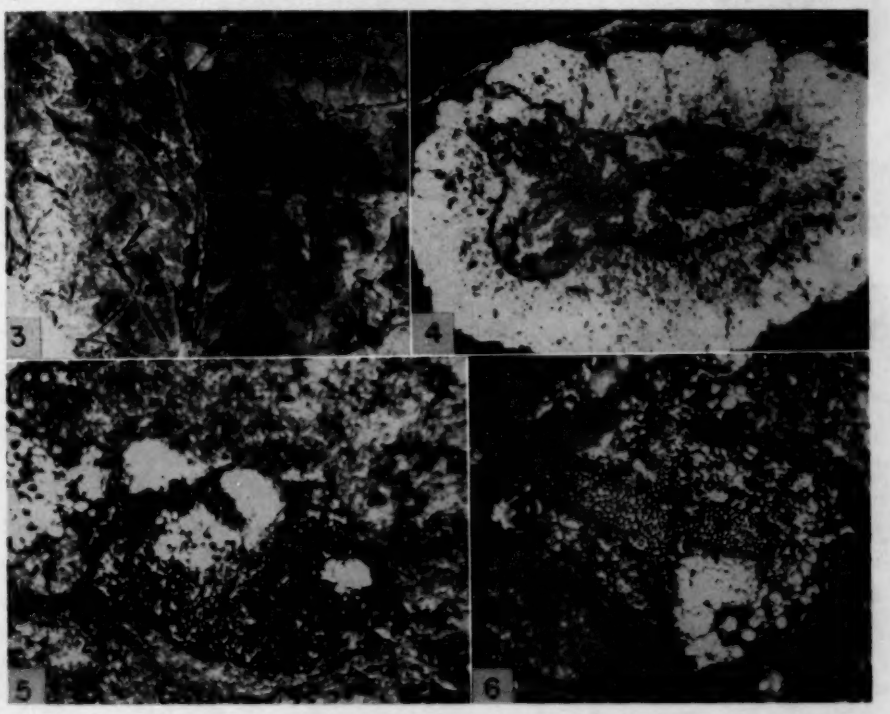


FIG. 3. A fossil plant compression of the type in which portions of some axes are structurally preserved by pyrite, × ¼. FIG. 4. A plant fossil embedded in a small pyrite concretion, × 11. FIGS. 5–6. Pyritized axes taken from a compression specimen like that shown in figure 3. FIG. 5. A crumbled, nearly useless, surface of a pyritized plant axis, resulting from an attempt to polish the surface before treatment with HSR, × 20. FIG. 6. A polished surface of an axis similar to that shown in figure 5 made possible by treatment with HSR, × 30.

has evaporated. Toluene is suggested as the more ideal solvent since it is more volatile than xylol and thus evaporates much more rapidly. Both have been used successfully. HSR is used by the writer primarily because he has a large supply available. Canada balsam, or other synthetic resins can be used with apparently equal success.

A knowledge of the optimum moment at which evaporation of the solvent must be stopped is the key to success in using this technique. If all of the solvent evaporates, the embedding material becomes brittle and will fail to serve its purpose of preventing a crumbling of the surfaces to be ground and polished. On the other hand, if the coating of HSR is too sticky, polishing will be impossible. The following test is suggested: Dip a needle into the embedding solution. Before the solution has completely cooled, pull it from the needle, roll it into a ball and pull it. If it breaks without visibly stretching, the solution is probably too brittle. If it stretches slightly before breaking but is not sticky to the touch, the optimum moment has been reached. In case of unsuccessful attempts, the process may be repeated without apparent damage to the fossil material.

(3) Remove the sections immediately. Rid them of excess HSR before cooling, or with a hot needle after cooling.

(4) Grind the surfaces with a #600 abrasive powder and polish by the use of chromium oxide. The coating of HSR tends primarily to hold rigid the crystals of pyrite and the pyrite cell casts projecting from the cut surfaces. Since there is little, if any, actual penetration of the fossil by the HSR, one must grind no deeper than is absolutely necessary to obtain a completely smooth surface. Grinding should be done on a slow-speed lap if possible. The polishing of the surfaces by chromium oxide should be done on a glass plate. Crumbling may occur at this point unless extreme care is exercised.

(5) Mount on a glass slide. After each section is washed, it should be dried with cheesecloth, dipped immediately into toluene or xylol and mounted in Permount or some other fast-drying mounting medium. The space between the cover slip and slide should be completely filled with the mounting medium.

This entire procedure will have taken only 2 or 3 hours. After the mounting medium has dried, the specimen can be examined on both sides by the use of reflected light, preferably with an Ultropak microscope. One can get a visual illustration of the value of this technique by comparing figures 5 and 6.

The value of studying pyritized plant fossils cannot be over-emphasized. The especial importance of studying petrified axes of compressions has been illustrated by the work of Leclercq (1951) on *Rachophyton*. The writer is convinced that the value of this kind of information is so great that a serious attempt to locate short lengths of petrified axes should be made by every paleobotanist when working with compressions. Use of the above technique will facilitate the study of these pyritized axes.

SUMMARY

1. The importance of studying structurally preserved portions of axes of compression specimens is stressed and several examples of previous work of this nature are cited.

2. Two common types of fossil preservation in pyrite are discussed.

3. A technique which facilitates the grinding and polishing of surfaces of pyritized plant fossils is described and its usefulness to the paleobotanist is emphasized.

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A CYTOGENETIC STUDY OF CERTAIN RACES OF *OENOTHERA ELATA*[1]

ERICH STEINER

In an earlier paper (Steiner 1951) reporting the results of cytogenetic analysis of five races of *Oenothera elata*, the conclusion was reached that this species was not ancestral to the North American oenotheras and was probably derived from *Oe. hookeri* or a *hookeri*-like ancestor. The current investigation of four new collections from central Mexico was undertaken to obtain additional evidence on the relationships among races belonging to *Oe. elata*.

All Mexican and Guatemalan euoenotheras so far studied cytogenetically are large-flowered, open-pollinated forms showing seven pairs of chromosomes at meiosis. Hybrids between different races, however, may show circles of chromosomes at meiosis. Therefore, many of the forms, although structural homozygotes, have undergone segmental interchange leading to distinctive arrangements of their chromosome ends. Such segmental interchange has occurred even more extensively among the North American euoenotheras concurrently with the development of the self-pollinating habit and a balanced lethal system; thus has resulted the peculiar cytogenetic mechanism for which *Oenothera* is so well known.[2] Through the work of Cleland and others, a system of chromosomal end arrangement has been established by which it is possible to assign to any given genome or "complex" a segmental arrangement in terms of the standard arrangement, 1·2 3·4 5·6 7·8 9·10 11·12 13·14.[3] Using Cleland's techniques, the genomes of the New Mexican collections have been analyzed for chromosomal end arrangement.

The segmental arrangements provide a convenient index of phylogenetic relationship, since there is evidence (Cleland, et al., 1950) that, in general, forms with the same segmental arrangement are more recently derived from a common ancestor than forms with widely different arrangements.

The determination of segmental arrangements of *Oenothera elata* should reveal the extent which the different local populations represented by our collections have undergone segmental interchange and whether the same segmental arrangement is characteristic of larger geographical areas. Further, if these forms represent derivatives of an ancestral population which

[1] Work supported by Faculty Research Fund of the Horace Rackham School of Graduate Studies, University of Michigan.

[2] For a brief account of this cytogenetic mechanism, see Cleland, 1949.

[3] Each chromosome is represented by two numbered ends joined by a dot.

also gave rise to the North American euoenotheras, it is of interest to seek evidence as to why, in spite of reciprocal translocation, no complex-heterozygotes have arisen in the Middle American region.

Materials and methods. The collections here investigated are shown in Table 1. The geographical distribution of all *Oe. elata* collections so far

TABLE 1. *Races analyzed in the current study*

Race	Collector	Source	Chromosome Configuration
Acatzingo	P. A. Munz	Acatzingo, Mexico	7 pairs
Cholula	"	Cholula, Mexico	7 pairs
Puebla	"	Puebla, Mexico	7 pairs
Puerto-aereo	"	Dis. Fed., Mexico	7 pairs

analyzed is seen in figure 1. Each of the new collections was hybridized with

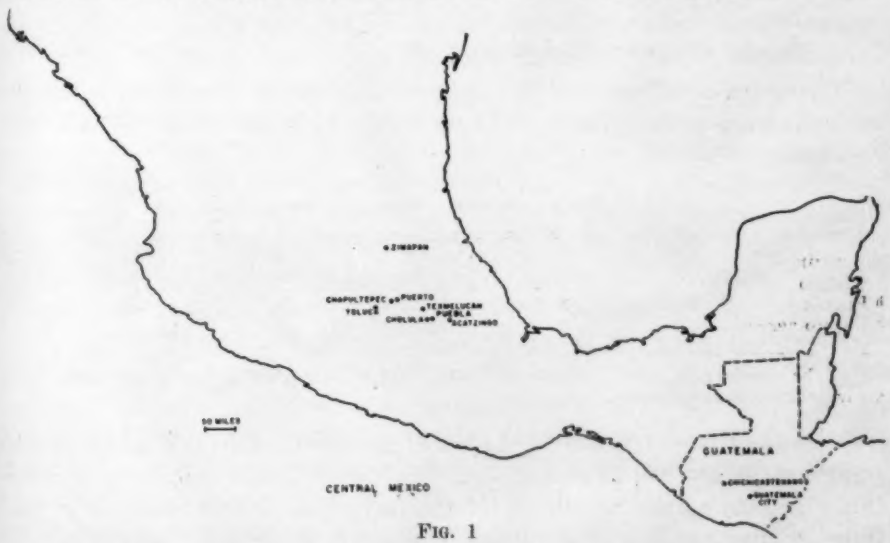

FIG. 1

a series of standard races whose complexes had previously been genetically and cytologically identified. The chromosome configuration of each hybrid was determined and from these configurations the segmental arrangements of the new races were worked out. An example of such a cytological analysis is given in the earlier paper (Steiner 1951). For further details regarding the methods used in the study of *Oenothera* phylogeny see Cleland, et al., 1950.

Observations. The collections *Acatzingo, Cholula,* and *Puebla* possess the following characters:

Leaves gray-green, elliptic-lanceolate, acute; typical lower cauline leaf, 11.5 × 2.5 cm.; surface slightly crinkled, strongly wavy; mar-

gins entire to obscurely toothed with appressed hairs; surface hairs moderately numerous, closely appressed; midrib white; pulvinus green.

Stems with no papillae, green basal color; tips below bracts green with a heavy felty pubescence.

Habit. Central shoot with numerous lateral branches often reaching the same height as the central shoot; only a weak tendency toward rosette formation when grown in Michigan.

Bracts strongly reflexed, green.

Buds. Typical cone, 2.9 cm. long, somewhat angular, tapered, typically 5 mm. thick at base, yellow green, thick-skinned with numerous, long appressed hairs; hypanthium typically 1.8 cm. long, yellow green; ovary typically 1.0 cm. long, gray-green.

Flowers 4.5 to 5.5 cm. in diameter; petals 2.5–3.5 cm. wide, 2–3 cm. long.

Height as grown, 98–130 cm.

Puerto-aereo differs from the above description in possessing moderate anthocyanin pigmentation in the base of the stem, the stem tips, and the bud cone.

TABLE 2. *Newly determined segmental arrangements*

^{h} Acatzingo*	1·4	3·2	5·9	6·8	7·10	11·12	13·14
^{h} Cholula	1·4	3·2	5·9	6·8	7·10	11·12	13·14
^{h} Puebla	1·4	3·2	5·9	6·8	7·10	11·12	13·14
^{h} Puerto-aereo	1·4	3·2	5·6	7·10	9·14	11·12	13·8

*The superscript "h" (haplo-) indicates that the complex occurs in duplicate in a structurally homozygous race.

Crosses of these forms with the North American races used as standards produced, in general, abundant seed which germinated readily to develop into vigorous, normal seedlings. Of the forty-four crosses made, only two failed to produce viable seedlings. The newly determined segmental arrangements are shown in Table 2. Table 3 lists those arrangements, determined previously, which occur in other races of *Oe. elata*. The segmental arrangement encountered most frequently among races of *Oe. hookeri*, the group considered to be ancestral to the North American euoenotheras, is also shown.

Discussion. The ten collections of *Oenothera elata* which have been analyzed cytogenetically show three distinctive chromosomal end arrangements. For convenience these will be referred to as the *Toluca, Puebla,* and *Guatemala* arrangements, although each is represented by two or more collections. The interchange relations of these types are shown in Table 4.

The *Puebla* arrangement is intermediate between that of *Toluca* and

TABLE 3. *Previously determined arrangements occurring in races of Oenothera elata*

h Guatamala	1 · 2	3 · 10	5 · 9	7 · 4	6 · 8	11 · 12	13 · 14
h Chichicastenango	1 · 2	3 · 10	5 · 9	7 · 4	6 · 8	11 · 12	13 · 14
h Chapultepec	1 · 4	3 · 2	5 · 6	7 · 10	9 · 14	11 · 12	13 · 8
h Texmelucan	1 · 4	3 · 2	5 · 6	7 · 10	9 · 14	11 · 12	13 · 8
h Toluca	1 · 4	3 · 2	5 · 6	7 · 10	9 · 14	11 · 12	13 · 8
h Zimapan	1 · 4	3 · 2	5 · 6	7 · 10	9 · 14	11 · 12	13 · 8
Arrangement encountered most commonly among races of *Oe. hookeri**:	1 · 2	3 · 4	5 · 6	7 · 10	9 · 8	11 · 12	13 · 14

* The *race, hookeri,* which has been used extensively in the genetic work with *Oenothera* belongs, of course, to the *species, Oe. hookeri.* However, this race possesses 7 · 8 and 9 · 10 chromosomes, rather than 9 · 8 and 7 · 10 which the majority of races belonging to the species carry. It should be emphasized that in this paper when we speak of the *hookeri* arrangement, we are *not* referring to the arrangement shown by the *race, hookeri,* but to the arrangement most commonly found among all the races of the species.

Guatemala. The collections from Guatemala are characterized morphologically by smaller, more wavy leaves and the absence of anthocyanin pigment throughout the plant; members of the *Puebla* group, with the exception of the red pigmentation, resemble closely the central Mexican races of the *Toluca* group. As shown by the map (fig. 1) *Acatzingo, Cholula,* and *Puebla* are the most southerly of our Mexican collections and therefore nearest to Guatemala. Thus the *Puebla* group appears to be more or less intermediate between the *Toluca* and *Guatemala* groups with respect to segmental arrangement, morphological characters, and geographical distribution.

The data obtained earlier (Steiner 1951) led to the conclusion that *Oe. elata* was derived from *Oe. hookeri* or a *hookeri*-like ancestor. With the discovery of the *Puebla* arrangement among races of *Oe. elata,* the question arises whether this conclusion is still tenable.

The problem was approached by assuming, in turn, the *hookeri, Puebla, Toluca,* and *Guatemala* arrangements to be ancestral and the others derived. In each case all phylogenetic sequences in terms of minimal number of segmental interchanges necessary to derive from the assumed ancestral form the different arrangements were determined. A comparison of these se-

TABLE 4. *Interchange relations of the segmental arrangements occurring in races of Oe. elata and the arrangement most commonly found among races of Oe. hookeri*

Toluca group	1 · 4	3 · 2	5 · 6	7 · 10	9 · 14	11 · 12	13 · 8
Puebla group	1 · 4	3 · 2	5 · 9	6 · 8	7 · 10	11 · 12	13 · 14
Guatamala group	1 · 2	3 · 10	5 · 9	6 · 8	7 · 4	11 · 12	13 · 14
Oe. hookeri	1 · 2	3 · 4	5 · 6	7 · 10	9 · 8	11 · 12	13 · 14

Toluca—two interchanges removed from the *hookeri* arrangement
two interchanges removed from the *Puebla* arrangement
four interchanges removed from the *Guatemala* arrangement

Puebla—two interchanges removed from the *hookeri* arrangement
two interchanges removed from the *Guatemala* arrangement

Guatemala—two interchanges removed from the *hookeri* arrangement

quences revealed that all require the same *number* of interchanges to derive the other arrangements. However, of these, only one recognizes the close relationship of the *Puebla* and *Toluca* types; this phylogenetic sequence assumes the *hookeri* arrangement to be ancestral. The relationship of the *Puebla* and *Toluca* forms is readily apparent from morphological and geographical evidence; thus it is felt that the sequence by which the segmental arrangements of these types were derived should also reflect it. For this reason, *Oenothera hookeri* or at least a *hookeri*-like form, appears most likely to be ancestral for the races of *Oe. elata* so far analyzed. The proposed phylogeny of these forms is shown in figure 2.

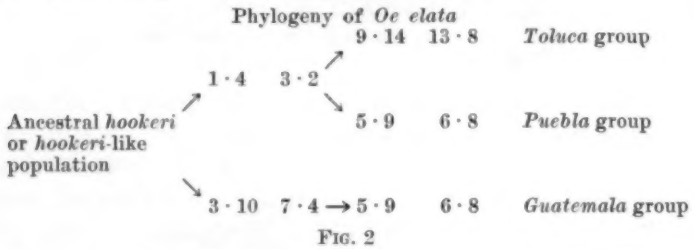

FIG. 2

Since the *Puebla* and *Toluca* type races are morphologically very similar and occupy adjoining areas in central Mexico, one may logically conclude that the ancestral form first gave rise in this general region to a type carrying the 1 · 4 and 3 · 2 interchange. The latter was in turn differentiated into the *Puebla* form toward the South and the *Toluca* type toward the North, in each case undergoing a single, but different interchange. In the Guatemala region the 3 · 10 and 7 · 4, and 5 · 9 and 6 · 8 interchanges arose directly from the *Oe. hookeri* population. This ancestral population must have originally been widespread, but later, probably as a result of climatic change, was fragmented into more or less isolated segments. These relatively small, isolated populations have since begun to differentiate. Munz' impression (personal communication) is that the *Oe. elata* populations do occur at rather scattered stations, which is exactly what one might expect to find according to the above hypothesis. The occurrence of small, isolated populations very likely accounts at least in part for the absence of ⊙ 14 heterozygotes in this area. Permanent translocation heterozygotes are thought to have arisen (Cleland, et al., 1950) through hybridization of the two populations which during a prior isolation had become widely different segmentally. This necessitates contact between populations once isolated. These Mexican races can be considered as presently undergoing segmental differentiation; if this continues and at some later date environmental change allows expansion and spread of the *Oenothera* populations, hybrids between different populations occurring at points of contact will be interchange heterozygotes with large circles of chromosomes at meiosis. With the development of the self-pollinating habit and a balanced lethal system, these

could become established as true-breeding heterozygotes. That such events may have occurred in midwestern and eastern North America seems plausible. In the latter areas the extensive environmental modification effected by man's settlement may have made available new habitats for previously differentiated populations of *Oenothera* to spread widely and hybridize, eventually producing balanced translocation heterozygotes.

It is also of interest to note that the 1 · 4 and 3 · 2 associations of chromosome ends which occur in all of the central Mexican collections are found in most of the beta *strigosa* (Cleland 1954), but not in any of the alpha *strigosa* complexes. Several of the beta *strigosa* complexes carry the 9 · 14 and 13 · 8, while only one alpha *strigosa* complex carries these chromosomes. On the other hand, the 5 · 9 and 6 · 8 occur among three of the twenty-seven alpha *strigosa* complexes so far analyzed. The widespread occurrence of the 1 · 4 and 3 · 2 in both the Mexican races and the beta strigosas indicates that these may both have been originally part of a population derived from the ancestral *hookeri*, the northern segment of which differentiated into the beta strigosas. In the absence of more extensive Mexican collections, however, such a suggestion may only serve as a working hypothesis when new material becomes available.

SUMMARY

1. Four new collections of *Oe. elata* from central Mexico have been analyzed cytogenetically.

2. Three of these possess the same arrangement of their chromosome ends, an arrangement not found among the previously analyzed races. The fourth has an arrangement identical with four other Mexican races described in an earlier study.

3. The segmental arrangements of collections of *Oe. elata* from Middle America are correlated with their geographical distribution and morphology.

4. The new cytogenetic data support the hypothesis suggested in an earlier study that *Oe. hookeri* or a *hookeri*-like ancestor was originally distributed throughout Middle America and that this population has been fragmented into relatively isolated segments which are currently undergoing cytogenetic differentiation.

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BULLETIN OF THE TORREY BOTANICAL CLUB

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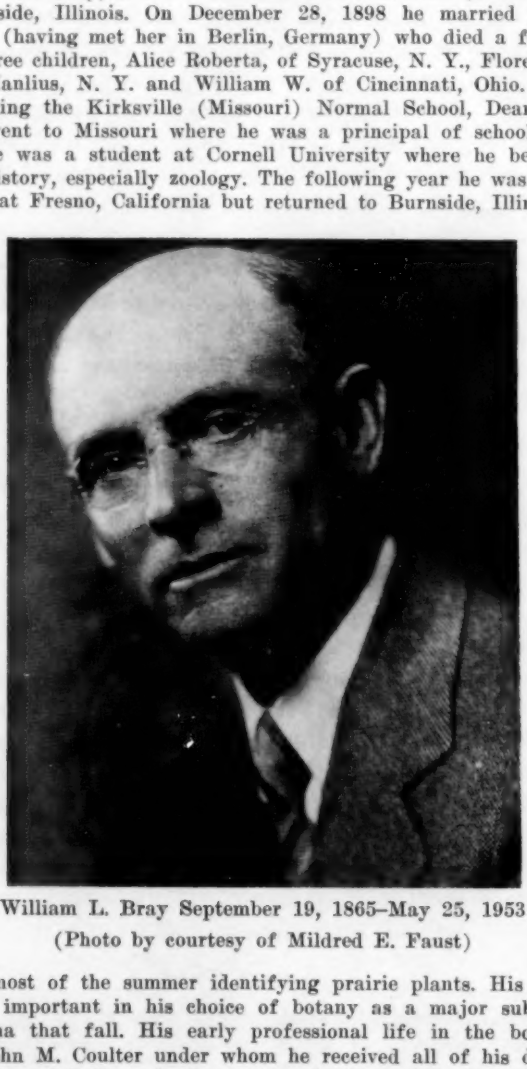
TORREYA

William L. Bray

Dean William L. Bray, son of William and Martha Ann (Foster) was born on a farm near Burnside, Illinois. On December 28, 1898 he married Alice Weston of Syracuse, N. Y., (having met her in Berlin, Germany) who died a few years ago. He is survived by three children, Alice Roberta, of Syracuse, N. Y., Florence (Mrs. Russell G. Fudge), of Manlius, N. Y. and William W. of Cincinnati, Ohio.

After attending the Kirksville (Missouri) Normal School, Dean Bray taught in Iowa and then went to Missouri where he was a principal of schools for four years. From 1889–91 he was a student at Cornell University where he became enthusiastic about Natural History, especially zoology. The following year he was general secretary of the Y.M.C.A. at Fresno, California but returned to Burnside, Illinois, in May 1892



William L. Bray September 19, 1865–May 25, 1953
(Photo by courtesy of Mildred E. Faust)

where he spent most of the summer identifying prairie plants. His adeptness in the use of keys was important in his choice of botany as a major subject at the University of Indiana that fall. His early professional life in the botanical field was guided by Dr. John M. Coulter under whom he received all of his degrees: the A.B. from the University of Indiana in June 1893, the M.A. from Lake Forest University (Illinois) June 1894 (a monograph on Amaranthaceae with Edwin Uline), and the Ph.D. at the University of Chicago in June 1898 (Vegetation of western Texas). While at Lake Forest he was instructor and adjunct professor of botany. In 1896-97

he studied and published under A. Engler at Berlin University, Germany. Upon completing his studies under Engler and at the recommendation of Dr. Coulter he accepted a teaching position at the University of Texas, where he remained for ten years. During this period he organized the botany department and became its first head, as well as doing a great deal of field work in Texas and Mexico. In January 1903 he was appointed chief of the Division of Forestry, Texas World's Fair Commission and during the following year visited many parts of Texas collecting woods for the Louisiana Purchase Exposition at St. Louis in 1904. Here he supervised the exhibit which was awarded the GRAND PRIX.

In 1907 he went to Syracuse University to establish and become head of the Botany Department in the College of Liberal Arts. In 1911 he organized the Agricultural Division in Syracuse University, which subsequently became the College of Agriculture. In the same year he also organized, and was appointed Acting Dean of the New York State College of Forestry at Syracuse University for part of the first year. He continued as an accessory instructor in Ecology for many years. He helped maintain a close bond between the Plant Science faculties of these three colleges in his chairmanship of "The Journal Club", an informal discussion group of current botanical research. He was so well regarded by the faculty and students of the College of Forestry that their first building was named "Bray Hall" in his honor. As a special investigator for the College he undertook extensive reconnaissance surveys and collections throughout the State which resulted in his publication on the vegetation of New York State. Due to his keen perception in the laboratory and field and his well-organized mind, all of Dean Bray's publications have remained of great value to the present. It is regretted that so able a man did not continue to publish and produce more research. However, his unpublished research was used in his classes and his influence was far reaching in his inspirational teaching and personal contacts with students. His friendliness and leadership encouraged fellowship between students and faculty. He enjoyed being "Daddy Bray" to the plant scientists.

He was appointed dean of the Graduate school in the College of Liberal Arts in 1918, served as dean of the College 1923–25, and retired from headship in the Botany Department in 1932 when his duties as dean increased, due to expansion of the graduate school to other Colleges. Syracuse University was fortunate in having such a profound scholar and administrator and expressed its appreciation of his contributions by conferring upon him the honorary degree of Doctor of Science in 1936.

He always felt close ties with the Torrey Botanical Club which he joined in 1908 and was given honorary life membership in 1937. He was a fellow of the A.A.A.S. and in 1937 made Emeritus-Life Member, which gave him great satisfaction. He was also a member of the Ecological Society of America, being in charge of the first summer meeting in the east, which was held at Syracuse, N. Y. in 1932 with the second summer meeting of the A.A.A.S. He belonged to the Botanical Society of America, the American Fern Society, and Sullivant Moss Society and the honorary societies of Sigma Xi, Phi Kappa Phi, and Phi Beta Kappa.

Dean Bray was active in creating interest in nature and helping in its conservation. After his retirement from Syracuse University in 1943 he continued to maintain an active interest not only in the University and its Plant Sciences Department but also in all botanists and botanical advancement.—MILDRED E. FAUST, Syracuse University.

The following are his botanical publications:

A preliminary synopsis of the North American species of *Amaranthus*. Bot. Gaz. **19**: 267–272; 313–320, 1894.

Synopsis of the North American *Amaranthaceae*. II., *Ibid.* **20**: 155–161; III., 337–344; IV., 449–453, 1895; **21**: 348–356, 1896. (With Edwin B. Uline.)

The geographical distribution of the *Frankeniaceae* considered in connection with their systematic relationships. Botanische jahrbücher für systematik pflanzengeschichte und pflanzengeographie. **24**: 395–417. 1897.

On the relation of the flora of the lower Sonoran zone in North America to the flora of the arid zones in Chile and Argentine. Bot. Gaz. **26**: 121–147. 1898

Relations of the North American flora to that of South America. Science (new series) **12**: 709–716. 1900.
The ecological relations of the vegetation of western Texas. Bot. Gaz. **32**: 99–217; 262–291. 1901.
Destruction of timber by the Galveston storm. The Forester **7**: 53–56. 1901.
Texas forests and the problem of forest management for the longleaf pine lands. Ibid. **7**: 131–138. 1901.
The tissues of some of the plants of the Sotol region. Bull. Torr. Bot. Club **30**: 621–633. 1903.
Forest resources of U.S.D.A., Bur. Forestry Bull. 47. 1904.
The timber of the Edwards Plateau in Texas. Ibid. Bull. 49. 1904.
Vegetation of the Sotol country in Texas. Univ. Texas Bull. 60. 1905.
Distribution and adaptation of the vegetation of Texas. Ibid. 82. 1906.
The mistletoe pest in the southwest. U.S.D.A., Bur. Plant Ind. Bull. 166. 1910.
The development of the vegetation of New York State. N. Y. State Coll. Forestry, Techn. Pub. No. 3. 1915. Revised Ibid. 29. 1930.
History of forest development on an undrained sand plain in the Adirondacks. Ibid. No. 13. 1921.
Botany and the State. An address at the dedication of the Biological Laboratory of the University of Texas on May 3, 1925. The Univ. of Texas Bull. No. 2545. 1925.

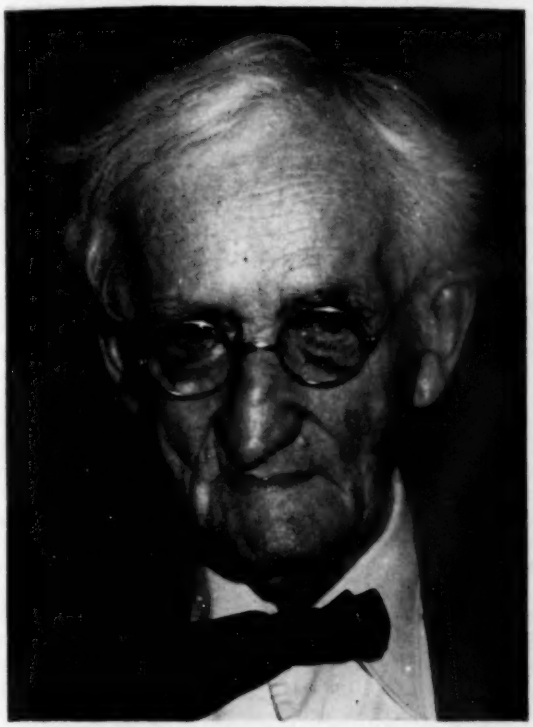
Liberty Hyde Bailey, the Botanist

When Liberty Hyde Bailey died at his home late Christmas evening, 1954, at the age of ninety-six, American botany lost what had been the last living link between the era dominated by Asa Gray, and the present. During the two decades now ended it was J. C. Arthur and L. H. Bailey who, among several thousand American botanists, could recount experiences of the Grayian era; with the passing of Arthur in 1949, Bailey stood alone in this niche. Everyone who knew Dean Bailey personally, or who was acquainted with his accomplishments over a life-time of ninety-six years, knew too that this man of stature was great for accomplishments in many fields of activity. A more detailed appreciation of Bailey and his major life-time accomplishments in many kinds of activities, together with a bibliography of books and vital statistics of his life, is to be found in BAILEYA (**3**: 26–40, 1955). The following paragraphs appraise and review his botanical work.

Bailey's first botanical paper (unsigned) was a review of a "Catalogue of Michigan Plants" (by C. F. Wheeler and Erwin F. Smith) published in the [Michigan Agricultural] COLLEGE SPECULUM in 1881. Characteristic of Bailey's concern for the application of botany was his comment, "The work is indispensable to every botanist; it should also be owned by every educated farmer in this State." Three years later the Torrey Botanical Club published in its Bulletin his first contribution of what was to become a series of twenty taxonomic papers on the genus *Carex*. One of these was the first number of volume one of the Club's Memoir series. For the period 1886–1905, Bailey was probably the dominant caricologist in America; collectors from Greenland to Alaska and southward to Panama sent him their specimens for determination. The *Carex* collections in the Bailey Hortorium herbarium are rich because of this material. Bailey's interest in *Carex* was encouraged by Asa Gray, with whom he worked at Cambridge (1883–84). Impressed at this time with the importance of type specimens to his *Carex* studies, he later won his demand from Cornell authorities (who sought him as a Professor of Horticulture) that they include an all-expenses-paid trip to Europe prior to his coming to Ithaca as a condition to his acceptance of the new position. The official reasons he gave Cornell's President for this trip are not known, but it is known that while in Europe he visited every important herbarium west of Russia, including those at Prague, Vienna, and Uppsala, and there studied and photographed *Carex* types. He used a cumbersome plate camera and had the plates shipped from Rochester, New York, to various European centers. (On one occasion German customs inspectors not only insisted on examining every unexposed plate in a dockside shed, but also tried to collect duty on the ruined negatives!) What is more important, the

glass-plate negatives of almost all of those 200-odd photographs are today in good condition. Bailey, while not the first American to study type specimens in Europe, probably was one of the first to bring back series of photographic negatives of the specimens studied. At this period, also, Bailey was called on to prepare treatments of *Carex* for various American manuals and local floras.

Through the influence of Sereno Watson of the Gray Herbarium, Bailey was engaged (1894) to revise "Gray's Field, Forest and Garden Botany." In doing so he added authorities for Latin names and more than doubled the number of garden and agricultural plants included. Throughout his lifetime, Bailey sought to bring the findings of botanical science within the grasp of the ordinary person. His "Talks Afield" (1887) was an explanation of botanical structures and functions written in



L. H. Bailey March 15, 1858–December 25, 1954.
(Photo by courtesy of Cornell-Photo Science Service)

the parlance of the farmer, amateur botanist, and youth. "Lessons with Plants" (1898) was a botany text written for students, but differed from existing works in that commonly known plants of the garden and field were used in discussion and to illustrate the text. His "Botany: an elementary text for schools" (1900), "Beginners Botany" (1908), and "Botany for Secondary Schools" (1913) were patterned along these lines. Financially they were successful; some were more widely adopted in Canada than in this country. A later book that had more appeal to the botanical novice than to the professional was his "How Plants Get Their Names" (1933), a work that went through only the one edition but whose content, although technical and erudite, was delightfully presented and deserved wider popularity. Wholly aside from the botanical and taxonomic character of his renowned "Standard Cyclopedia of Horticulture (1914–1917)[1], there are other books, more generally treated as horticultural rather than botani-

cal, whose contributions to the taxonomy of cultivated plants were considerable. Notable among these are his "Manual of Cultivated Plants" (1924, with its completely rewritten edition of 1949), "The Cultivated Conifers in North America" (1933), and a quartet composed of "The Garden of Gourds" (1937), "The Garden of Pinks" (1938), "The Garden of Larkspurs" (1939), and "The Garden of Bellflowers" (1953) —each a horticultural monograph, complete with keys to species and taxonomic discussions of taxa concerned. Each of these works represented considerable taxonomic study by Dr. Bailey. Indigenous material of taxa involved was studied at leading American herbaria, original descriptions were often consulted, and occasionally loans were requested from foreign sources. Conversely, Bailey himself would be the first to make clear that the treatises were not taxonomic revisions in the botanical sense; the scope was too limited, little study was given to matters of detailed distributions, no resolution was attempted of taxonomic problems associated with non-cultivated congeners, and no attempt was made to resolve relationships within infrageneric taxa above the rank of species. Nevertheless, each is a contribution of considerable value to the horticulturist and is one to be consulted by botanical monographers in the future.

Aside from these horticultural applications of taxonomic study, Dr. Bailey's botanical contributions have been associated, since the turn of the century, principally with taxonomic studies of the New World palms (plus a few genera of the Old World tropics), and the genera *Brassica*, *Vitis*, *Cucurbita*, and *Rubus*. Most of his papers on these plants have been published in GENTES HERBARUM, a periodical now in its eighth volume, founded by Bailey in 1920, financed by the New York State College of Agriculture at Cornell since 1930, and currently edited from the Bailey Hortorium.

Bailey's interest in palms began with his visit to Jamaica in 1910, and his first taxonomic paper on them was published in 1930. From then until 1949 he published 45 papers on members of the family, two of which are floristic, "Palms of Panama," "Indigenous Palms of Trinidad and Tobago," and the remainder revisionary or monographic in scope. Notable among these are his revisions of the genera *Acrocomia*, *Arecastrum Brahea*, *Butia*, *Coccothrinax*, *Copernicia*, *Erythea*, *Roystonea*, *Sabal*, *Thrinax*, and *Washingtonia*. Bailey's initial palm studies showed immediately the inadequacy of existing herbarium specimens. New collecting techniques were developed by him, to the extent that his palm herbarium at Ithaca, now occupying more than eighty steel herbarium cases, has become one of the finest, if not the largest, anywhere. It is the result of more than twenty collecting trips to Mexico, Panama, Venezuela, Brazil, Colombia, and scores of islands of the West Indies. Always an exponent of the importance of good photographs to taxonomic studies, he carried a view camera with him on his trips, and the herbarium record contains hundreds of photographs of palms represented in his collections. For many years Dr. Bailey planned as his *magnum opus* a comprehensive treatment of the palms of the world. Summing up his views on this a few years ago, he slapped his hand on the table and said, "Of course it will be my unfinished symphony, but it is wonderful to work at." He did work at it. When he fell in a New York City bank on December 29, 1949, and broke his upper thigh, he had in his pocket a one-way series of tickets from New York to the oil-palm country of the Belgian Congo, letters of introduction, and specific instructions for the disposal of his remains and personal effects should he not live to return; date of departure: January 2, 1950. Those flight reservations were cancelled December 30, 1949.

Bailey's work in the genera *Cucurbita*, *Brassica*, and *Vitis* is less well known than that in the palms and *Rubus*. However, time may prove these studies to be among his best, especially the revisions of *Vitis* and *Brassica*. These studies were based on intensive field

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[1] Confusion has been injected into the literature citations for this work, due to the publisher's practise of treating subsequent printings as later editions. The work was first published in six volumes in 1914–1917. A 2nd edition published in 1922 differed only in the correction of misprints and typographical errors. All so-called editions published after 1922 have been printed from the original plates of the 2nd edition, and it is incorrect to cite these dates or later reprintings as if they were of revised editions of same.

work as well as studies in the herbarium. Bailey's *Brassica* material was collected by him along the coasts of Great Britain, and western Europe, from eastern and central China, and from marketplaces of four continents. For more than forty years he grew and studied the cultigens of the genus, selfed the cultures, made crosses and back-crosses, and kept good records of his studies, including vouchers for the herbarium. Similarly with the cucurbits, he collected material from the backlands of Mexico, from isolated tribal plots of the Seminole Indians, and from Panama and northern South America. His earliest records of crosses and varietal studies in the group date from 1886, started at Michigan State College. Through the years, his active interest in the group never waned. In 1949, the Hortorium garden at Ithaca was overrun with cucurbits—on the fences, across the walks, and among plants grown for study by other members of the staff. The *Vitis* paper was preceded by extended collecting trips from Missouri along the Gulf to Florida, and northward. In the earlier days, he worked actively with Munson, then a leading authority on the genus. As was true for *Carex*, so too for *Vitis* he contributed treatments of the genus for various American manuals and floras.

Dr. Bailey placed his taxonomic studies of *Rubus* at the top of his accomplishments in systematic botany. These studies began before 1890, when he published a series of three papers on the native dewberries. This was followed in 1895 by an extensive treatment of the cultivated blackberries and their indigenous counterparts. However, it was not until 1932 that he published his first major monographic treatment in the genus, and during the period from March, 1941, through November, 1945, he was busy with the publication of his *opus*, "The Genus Rubus in North America." There were also other notable *Rubus* papers, treating species of the West Indies and South America, and two substantial Supplements to the Monograph (1947, 1949). The *Rubus* herbarium at the Hortorium numbers in excess of 33,000 collections, of which the great majority were made by Bailey. As for the palms, here, too, he demonstrated the need of having adequate and representative herbarium material, including that from the first-year canes as well as from the second-year flowering canes. Bailey considered the genus *Rubus* to contain 487 species for North America. By most botanists, not themselves so familiar with the genus in the field, this number is considered excessive.

In an appraisal of this and other taxonomic studies by Bailey, one must consider his basic species philosophy. He was an evolutionist in every sense of the term. At the same time, he treated the nomenclatural type of a species as one taxon and variants of that species as satellites or appendages of it. This was the concept of such men as Gray, Hooker, Reichenbach, Jepson, and Merrill. It is a concept that does not consider the species as a biological unit, its nomenclatural type holding that position only because it happened to be the first to be named and described with the binomial. When Bailey described a species having one or more varieties, other than the typical component, his description accompanying the binomial was only of the typical element. Having done this, he proceeded to describe the varieties as adjuncts. He did not accept the view now prevalent among botanists that the description of the binomial should cover all taxa included within it. For him, a species might have varieties, but it was not composed of varieties. Bailey recognized only one infraspecific category, that of VARIETAS, and never subscribed to the view that knowledge of the kinds of plants was enhanced by treating the species as composed of subspecies, and subspecies as composed of varieties, and the varieties of forms.

Bailey had definite ideas on the subject of hybrids and hybridity. It has been reported that he did not accept the existence of hybrids in nature, that in his *Rubus* studies he treated them as species, and that he rejected summarily the opinions of others when they described hybrids in *Rubus*. These allegations are not wholly true. Not only did Bailey accept the existence of hybrids in nature, but he described some as such and gave their parentage. In his revisionary studies, however, he challenged every previous worker's statement if hybridity was alleged to exist. To Bailey, the intermediacy of characters was of itself insufficient evidence of hybridity; he insisted on geographical proximity and evidence of genetic compatibility in nature, of the alleged parents. He felt that, too often, the imputation of hybridity was used by the taxonomist as a cloak to cover igno-

rance. In his earlier years Bailey was a leader in the subject of plant-breeding (in fact, he coined that phrase), was the author of three text-books on the subject (the first published in 1892) and of many papers during that period. However, it cannot be said that he was a geneticist. His activity in the field ended at about the turn of the present century. This was before the gene theory was propounded and before the intricacies and significance of chromosome activities were well understood. Although he read cytogenetic literature, tried to understand without bias the objectives and accomplishments of the cytogeneticist, and consulted published data on the subject as concerned the taxa with which he worked, he did not always appreciate the importance to taxonomic conclusions of such phenomena as polyploidy, autoploidy, amphiploidy, and apomixis.

Bailey was not without his reasons in these opinions on cytogenetics as they relate to taxonomy. On several occasions he demonstrated the folly of reliance on published chromosome counts where verification of the correctness of identification of the material concerned was impossible because the cytologist had no vouchers of the plants with which he worked. To help to offset this deficiency, he encouraged cytogeneticists and cytotaxonomists to prepare vouchers to their material and ensure their preservation in herbaria; the increasing number of collections of this character now deposited in the Bailey Hortorium attests to his efforts in this direction. In his last years he engaged Dr. John Einset, a competent cytogeneticist, to grow plants of *Rubus* collected by both of them from the wild. The cytological studies that followed demonstrated the existence of apomixis in some of the taxa and clearly indicated hybridity in others. It is to Bailey's credit that he arranged for the publication of the initial studies in this work in GENTES HERBARUM. It is unfortunate that this information for the genus *Rubus*, prepared, of course, on a much broader scale, had not been available to him a decade or more previously. The data came to him at a time when his monograph was completed, when his ideas and concepts were crystallized, and when he had passed the peak of his performance. It was at a time before the rules of nomenclature had accepted the apomict as a taxonomic category, or had made provision for its accounting. Bailey did not reject the existence of apomicts. Following Einset's work, he held the view that if some of the taxa he named and described as species are apomicts, or are proven hybrids, it is for subsequent workers to relegate them to their proper place and to treat them nomenclaturally as provided by the Code. In his monograph he has directed attention to morphological dissimilarities in these taxa, has documented locations where they are indigenous, has typified each, and has paved the way for subsequent workers (probably cytotaxonomists) to clarify the biological picture. Time will decide whether his nomenclatural separation of these plants, and his focusing of attention on their differences, are a greater contribution to the ultimate solution of the problem than is the wholesale "lumping" of taxa without any investigation of the biology of the alleged aggregate species.

The turmoil in botanical nomenclature in which American botanists were involved more than a half century ago is now history. But it is noteworthy that, in a period when his principal activity was in horticulture and agriculture at Cornell, Bailey took a major part in those controversies. Initially he was a member of a committee active in formulation of the Rochester Code. Although trained in part under Asa Gray, he supported Britton and the view that the principles of *nomina generica conservanda* and of the so-called "Kew Rule" were scientifically unsound. His support of the nomenclatural-type-concept was ardent and enthusiastic. As early as 1887 he published on the subject and in the same year proposed corollary rules for horticultural nomenclature. Two years later he wrote a U.S.D.A. Circular comprising "Rules for Naming Vegetables." However, largely as a result of two extended trips to European botanical centers in the late 1890's, he conceded that the European botanists were unlikely to accept Britton's rigid nomenclatural proposals. Following this, he urged adoption of conciliatory measures that would result in a code of nomenclature acceptable at the international level. He argued that, as botanical study was without national boundary, so also must the rules of nomenclature be international if world-wide stability of scientific names was to be achieved.

No review of Liberty Hyde Bailey's botanical contributions can omit consideration of his impact on the science as a man. His personality and character were just

as individual as his name. While he read avidly with an open mind, and sought continually to expand his horizons, he reached conclusions by himself and stood by them. Seemingly, he lived to accomplish. On New Year's Day, or the night before, he would list the items of research, travel, and publication that he would strive to accomplish during the coming year. This list would sometimes hang from a nail in the "palm room" at the Hortorium. He would list titles of books yet to be written, and had a folder of notes and outlines of their contents, of work to be done in the course of their preparation. On the other hand, he kept no record of what he had done, no list of books and papers published, no diaries of his living (aside from two written in his youth, a few journals of his travels, and his plant collection note-books). In this regard, he once commented, "I have no time to record history; my interest is in the future." With this viewpoint, he wrote no memoirs, no accounts of his travels.

This submersion of ego did not mean that he lacked pride or vanity. He was a tall man of medium build, who walked erect and vigorously. He dressed well. From middle-life onward, he usually wore a conspicuous broad-brimmed hat, usually pale tan or black in color. When Dean of the College of Agriculture, he prided himself upon being driven in his buckboard with as fine a span of horses as could be had. He was a man of direct speech, sometimes blunt to the point of rudeness, and even more he was a man of direct action. He usually answered a letter the day it arrived. He would have been happy if his directives could have been completed the day before they were given. Just as he had the gift of writing in a delightfully flowing style of prose, so also did he have a gift for oratory. As late as 1949 he would hold student audiences at Cornell enthralled, and always there was a message, often with a bit of sting, in what he had to say. He could sense the pulse of an audience of 5,000 as well as one of a handful of persons, and his public addresses given in every state of the country numbered in the hundreds. One quality of Bailey that impressed all who have been associated with him, or who have come to him for counsel, was his tolerance for the opinions of others and his understanding charity toward his critics. Many times, when working on Hortus Second, a colleague would encounter a recent taxonomic work where the conclusions were contrary to those proposed earlier by Bailey. Sometimes Bailey would be advised of them and asked for an opinion. The usual answer was, "Of course, we must follow Jones. His evidence is more complete and better than any I had!" Some of the published criticisms of his *Rubus* studies were caustic, or barbed with inuendo. While Dr. Bailey would have preferred the author to have raised the challenges in person or through correspondence, he never expressed feelings of bitterness, and certainly not of recrimination or anger. Throughout the years he was always ready to set aside whatever he was doing to give counsel or advice to those who sought it. He was not one to show impatience on being interrupted for good cause.

Liberty Hyde Bailey may stand in the annals of botanical history as a productive man of great intellect, of forceful drive and personality, who, more than any of his colleages, labored diligently so that, through the efforts of the botanical fraternity, his fellow man might be better informed on the kinds of plant about him. Bailey was a botanist in his own right. But more than that, he was the common man's botanist in that he applied the findings of his chosen science to the plants of the garden, of the cultivated fields, and of the forests. Mankind is richer by his labors.—GEORGE H. M. LAWRENCE, Cornell University.

Albert Francis Blakeslee

The sciences of botany and genetics lost a keen and energetic leader in the death of Albert Francis Blakeslee in his 81st year on November 16, 1954 in Northampton, Massachusetts. After retiring in 1941 as Director of the Department of Genetics, Carnegie Institution of Washington, Cold Spring Harbor, N. Y., A. F. Blakeslee accepted an invitation from Smith College to be the William Allan Neilson research professor of botany. At the age of 68 he set out with characteristic vigor to obtain research grants and to establish and direct the new Smith College Genetics Experiment Station. During the following twelve years nine graduate students working with him completed their

master's degrees and four received the Ph.D. degree. At the same time an extensive research program was carried out resulting in over 70 publications by the staff.

A. F. Blakeslee was born in Geneseo, N. Y., November 9, 1874, the son of a Methodist minister. He was graduated from Wesleyan University, obtaining his A.B. degree cum laude, in 1896. Undergraduate recognitions included election to Phi Beta Kappa, prizes in mathematics and chemistry, a college tennis championship, and a letter in football.

After three years of teaching sciences and mathematics at the preparatory school level he began graduate studies at Harvard University and a year later, in 1900, received his A.M. Research in mycology, carried out under Professor Thaxter, led to completion of his doctoral thesis "Sexual Reproduction in the Mucorineae." He received the Ph.D. degree in 1904 and his thesis, published the same year, earned immediate recognition for the important discovery of sexuality in the lower fungi and for the revolutionary effect this had on understanding sexual reproduction among the lower plants.

A. F. Blakeslee, November 9, 1874–November 16, 1954
(Photo by courtesy of Harold H. Smith)

As a result of his many scientific achievements, Dr. Blakeslee was awarded honorary doctor's degrees from the University of San Marcos (Peru), University of Delhi (India), Yale, Smith, Wesleyan, University of Paris and the University of Arkansas.

From 1907 to 1915 he was professor of botany at the Connecticut Agricultural College, Storrs, Connecticut. During this time he began studies on a variety of experimental materials including the domestic fowl, *Rudbeckia*, Adzuki beans and *Datura*. The book "Trees in Winter" was published in 1913.

In 1915 Dr. Blakeslee accepted a position as resident investigator in plant genetics at Carnegie Institution, Long Island, N. Y. In 1923 he was appointed Assistant Director, during 1934–35 he was Acting Director, and in 1936 he became Director.

Albert F. Blakeslee married Margaret Bridges in 1919. She died in 1947. They had no children.

His main research interest through the years was concentrated on the genetics and cytology of *Datura stramonium* and the nine other species of the genus. The tetraploid form of this plant was found and studied early in the program. In 1921 the trisomic mutant "Globe" was reported and the following year the haploid form was described, the first haploid higher plant known. His investigations on extra-chromosomal types and the role played by each chromosome in inheritance are genetical classics. In collaboration with the late Dr. John Belling, he was the first to demonstrate the interchange of segments between non-homologous chromosomes and the consequent cytological differences by which these could be recognized. In 1937 he began a series of publications on the effective use of colchicine to increase the number of chromosomes in plants. This opened up a far-reaching field of investigation on artificially-induced polyploidy which had both theoretical and practical implications.

Chief emphasis of the *Datura* work at the Smith College Genetics Experiment Station was on genetical and physiological investigations of incompatibility in species crosses including detailed studies of ovule and embryo development. On the basis of the *Datura* research Dr. Blakeslee won prizes awarded by the New York Academy of Sciences, the Palais de la Decouverte (Paris), and the Massachusetts Horticultural Society.

Albert F. Blakeslee's interests also extended into problems of human genetics. He studied differences in ability to taste and smell and traced their inheritance through families. Phenyl-thio-carbamide (PTC), mannose, and other chemicals were used in the taste tests and flowers, such as Freesias and Verbena, to test smell.

He and his research associates contributed over 300 scientific articles and many of these were delivered as papers or demonstrations at congresses and society meetings where he was a familiar figure.

In addition to research activities A. F. Blakeslee found time to act as Director of the National Science Fund; Visiting Lecturer in Genetics at Harvard (1948–49); and member of the National Research Council, the Trustees of "Biological Abstracts," and the Board of Managers of the New York Botanical Garden.

He was elected to membership in the National Academy of Sciences and the American Philosophical Society. Among the other scientific societies of the United States of which he was a member he held offices in the American Association for the Advancement of Science (President, 1940), American Society of Naturalists (President, 1930), Botanical Society of America (President, 1950), Human Genetics Society (Vice President, 1953), Society for Study of Development and Growth (President, 1946) and Torrey Botanical Club (Assistant Editor, 1924; President 1953). He also held membership in the American Eugenic Society, American Genetics Association, Association for Research on Human Heredity, Genetics Society of America, New England Botanical Club, Phi Beta Kappa Society, and Sigma Xi.

Dr. Blakeslee was a member of the following foreign scientific societies: Botanical Society of India; Genetics Society of Japan; Institut de France, Academie des Sciences; Linnean Society, London; Moscow Society of Naturalists (honorary); Mycological Society of Leningrad (honorary); National Institution of Science of India (honorary); Nederlandsche Botanische Vereniging; Royal Academy of Belgium; Royal Danish Academy of Science; Royal Physiographical Society of Lund, Sweden; Royal Swedish Academy of Science; Société de Biologie de Paris; and Sociétée Royal de Botanique de Belgique.

It was characteristic of A. F. Blakeslee that he enjoyed association with a group of researchers and many of his technical papers were in joint authorship with one or more cooperators. Althogether he published with 54 different co-authors. The loyalty engendered among those who worked closely with him is exemplified by the 30 years of cooperative research by Miss Sophie Satina. They were co-authors on about 35 publications. A number of young assistants worked under Dr. Blakeslee and to those who showed interest he gave attention and encouragement.

Albert Francis Blakeslee will be remembered for his contributions to the sciences of botany and genetics, uniquely so in the latter since his research career coincided closely to the first fifty years of its development. A colorful personality, he gave generously of

his time and of himself to his chosen profession and to the institutions with which he was associated.—HAROLD H. SMITH, Cornell University.

BOOK REVIEWS

North American Prairie. By J. E. Weaver, Johnsen Publishing Co., Lincoln, Nebraska. xii + 348 pp. 87 figs. 1954. $5.00.

This work constitutes an excellent summarization of studies of vegetation which have been conducted within the area which has been designated as the "true prairie" (*Stipa-Sporobolus* Association) by Weaver and Clements.[1] This unit of grassland extends from northern Texas to southern Manitoba between the oak-hickory section of the deciduous forest and the mixed prairie (*Stipa-Bouteloua* Association) of the drier grassland to the west. A comprehensive treatment of the ecology of this grassland area is only possible because of the tremendous effort which the author has expended in investigations of autecology and synecology during the past four decades in eastern Nebraska and the adjoining states. These investigations have resulted in scores of papers which have been drawn upon heavily in the present book. Weaver's contribution to the knowledge of grassland ecology in the eastern Great Plains should not be measured only by the fact that he has been associated with, or has stimulated his students to conduct, the investigations which resulted in about one-half of all the research papers which have been prepared concerning the vegetation of the region. In addition, we must take into account the fact that each of his projects has been much more extensive than most of the others mentioned.

This book has been prepared in a way which will make it interesting reading for all those who are interested in the general subject, without decreasing its value to those who are seeking detail. Even an intimate knowledge of Weaver's research papers will not reduce the value of the book to the readers, for here the various phases of grassland ecology are carefully interwoven. The numerous illustrations of habitat, plant and parts of plants are superb.

While a complete list of the subjects discussed would be too lengthy to present here, the following items are included: a general treatment on the nature of grassland and grasses (which has comprised the introduction to Weaver's well-attended courses at Nebraska), a discussion of the composition of plant communities of prairie, the ecological relations with the habitat (both aerial and edaphic) of each of the principal grasses and forbs, the effect of various environmental factors on the vegetation, the effects of the presence of plant cover in modifying the habitat, and plant-soil relationships. One-third of the text is devoted to the story of the effect of the drought of the 1930's on prairie vegetation. Fortunately, Weaver had just completed his extensive investigation of the composition and classification of communities of upland virgin prairie before the drought began in 1934. He seized the opportunity to continue his work throughout the drought in the sites he knew so intimately. These records have permitted Weaver to make a contribution which may never be duplicated in the rapidly decreasing extent of native grassland on the Earth's surface.

The ultimate aim of grassland ecologists will be to attempt to simulate Weaver's work in the other five or six major units of the North American Grassland and in grassland elsewhere.—R. T. COUPLAND, University of Saskatchewan.

Contributions to the Morphology of the Delesseriaceae. By Florence S. Wagner, University of California Publications in Botany 27: 279–346. Ill. Berkeley and Los Angeles.

The morphology and reproduction of comparatively few members of the Delesseriaceae are known. More than half of the genera in the family have not been investigated,

[1] Weaver, J. E., and F. E. Clements. Plant Ecology. 2nd Ed. McGraw-Hill Book Co., Inc., New York. 1938.

or they need reinvestigation. Many of the members of the family are rare or grow in remote areas of the world. Knowledge of the morphology and ontogeny of the group will help in understanding the relationships within the group and establishing a satisfactory classification.

The present work is a valuable addition to our understanding of the Family. Detailed information on the structure of the thallus and the development of the reproductive organs are included for representatives of 13 genera, none of these having previously been investigated and reported. Excellent figures are given showing details of the thallus development and stages in the growth of the reproductive organs. The genera included here are: *Branchioglossum, Bartoniella, Phitymophora, Botryocarpa, Holmesia, Marionella, Laingia, Abroteia, Neuroglossum, Polycoryne, Hymenena, Botryoglossum* and *Gonimophyllum*. A bibliography is included.—EDWIN T. MOUL, Rutgers University.

The Plant Quarantine Problem. By W. A. McCubbin. Chronica Botanica. Waltham, Mass. 1954. $4.80.

The appearance of this book is the first successful culmination of such directed efforts on the subject of plant quarantines operation in the United States. Rumors and reports of the imminent completion and publication of other comprehensive treatises on this subject have thus far not progressed beyond expectation. This document is a fitting and most welcome climax to a career embracing 31 years of intimate and perplexing association with the administration of plant quarantines, both State (Pennsylvania) and Federal.

The level of presentation is for the laity. This reviewer is of the opinion that the idea to attempt to educate the American public, affected directly or indirectly by plant quarantines, had its genesis in the author's harrowing experiences (1920–1925) during the early years of the enforcement of the State Potato Wart Quarantine in Pennsylvania. Much to the official dislike, the services of local sheriffs were frequently solicited to compel compliance by individuals who stamped such action as an invasion of their property rights. The necessity of such drastic action to safeguard the potato industry of the Northern United States was beyond the immediate comprehension of these aggrieved property owners. Can public education with the hoped-for end products of acquiescence and cooperation be substituted for compulsion? Can resistance and defiance be mellowed into a sympathetic understanding? The author with an affirmative faith was impelled to incarnate his ideas into this book which should serve as a medium for dissemination of information pertaining to the needs, objectives and administration of plant quarantines.

Accordingly the book carries chapter titles: biological background, social and economic relations, legal features, administration aspects, current quarantine problem examined, appraisal and outlook world situation, and a historical summary of Federal plant disease quarantines.

Three hundred pages comprise this book. The paper quality is excellent; the typography is designed for easy reading. The chapter titles are embellished by unique and attractive head pieces.

Various channels of communication of this plant quarantine information to the citizenry of this Country are suggested by the author. The biology department of the high schools and colleges, the vocational agricultural schools and the garden clubs should become centers of dissemination of such information. Practically every community in the country is located in an area where plant quarantines are operative. The acquaintanceship with the local quarantine enforcement should serve as a foundation to an understanding of national and interational involvements.

Colleges and Universities offering courses in economic entomology and plant pathology will undoubtedly welcome this book as a long overdue aid to their teaching. Instruction in this important aspect of plant disease and insect control has been inevitably perfunctory because of the necessity to organize a presentation from a widely scattered array of unconsolidated material. And, if the instructor is devoid of, or of limited ex-

perience in the field of plant quarantine administration he may be insecure in his interpretations.

To the plant quarantine administrators and inspectors (for whom the book is not primarily intended) this book may appear very elementary. Nevertheless, morsels of revealing, provocative and useful information will be frequently encountered as the treatise unfolds. This book records the perspective of a seasoned, experienced and thoughtful colleague, and as such a reference for future re-examination. Oral declarations on this subject, even though of currently recognized import, are subject to evanesence and ultimate oblivion.

Mr. McCubbin embarked on an educational project, aided by his book as the vehicle, to "present the subject as a whole, bringing together all its aspects in such form as to constitute an overall review." This objective has been admirably attained. The bibliography is the most extensive since the Brookings Institution, U. S. Government Service Monograph No. 59—"Plant Quarantine Control Administration" published in 1930.

The extension of the appendix to include a comparable discussion of some of the insects (Japanese beetle, Gipsy moth, white fringed beetle, Mediterranean fruit fly) which are now the subject of plant quarantines would have added to its completeness.—EDGAR G. REX, New Jersey Department of Agriculture.

Plant Physiology. By Jacob Leavitt. 156 pages. illustrated. Prentice-Hall. 1954. $5.00.

This book, intended for a one semester course of some thirty lectures, cannot treat with all the topics frequently considered in the province of plant physiology. The topics chosen reflect both the author's own interest and a modern trend in undergraduate courses in plant physiology to emphasize cellular physiology and biochemistry.

The Introduction (Part I) consisting of 11 pages, emphasizes the dependence of physiology on the basic concepts of physics and chemistry and some of the features of cellular structure and function which are basic to the concepts introduced later.

Part II, 60 pages, is called Plant Biophysics and Biophysical Chemistry. It includes chapters on Hydrogen-Ion Concentration, Surface Forces, and Other Colloidal Phenomenon, Diffusion and Osmosis, Permeability, Adsorption, The Ascent of Sap, Translocation of Solutes, and The Exchange of Gases. These topics are in the area of the author's research interests and are presented in a clear and interesting fashion.

Part III, 40 pages, is entitled Plant Biochemistry and includes Nutrition, Metabolism, Respiration, Photosynthesis and Other Aspects of Metabolism. The fourth part of the book is entitled Growth and consists of 23 pages in 4 chapters: Growth, Growth Movements, Growth Substances, and Development.

Appended to each chapter is a list of references, to original sources in journal articles, review articles and monographic treatments. The references are well chosen to deal adequately with the topic concerned. The author in his textual treatment moves rapidly from a descriptive level to the introduction of important but difficult concepts which require some, and often, considerable background information to understand fully. These concepts are not developed at length in this rather brief treatment. Hence the student with an inadequate background will find it necessary to read extensively in the reference literature to round out a thorough understanding of the subjects covered in the text.

The book is attractively printed and bound, and is written in a clear and interesting fashion.—JAMES W. MARVIN, University of Vermont.

Outlines of Enzyme Chemistry. By J. B. Neilands, Department of Biochemistry, and Paul K. Stumpf, Department of Plant Biochemistry, University of California, Berkeley. John Wiley and Sons, Inc., 440 Fourth Avenue, New York 16, N. Y. 1955. x + 315 pp. $6.50.

This book is intended for beginning graduate students and for research workers in fields other than enzymology. Not only is it well suited to this audience but will un-

doubtedly be read with interest by enzymologists. Here is a concise but surprisingly complete coverage of the basic principles written in a clear and readable manner.

The subject is developed under four main headings: General Principles, Physical Chemistry, Types of Coenzymes, and Enzymes and Metabolic Patterns. The approach is that of workers in the field. Consideration is given to the experimental methods and interpretation of observations as well as the shortcomings and difficulties of the methods and indication of the questions unanswered. By use of specific examples of experimental data, the reader is exposed not only to the principles of enzyme chemistry, but also to their development and application. For those topics which require mathematical treatment the authors have included simple algebraic manipulations so that the reader may direct his attention to the purpose of the manipulations and the ideas being developed. As each topic is developed, well selected reference to review articles and recent literature provides a means for a more detailed development as it is desired. The blend of practical and theoretical arouses interest and prevents the subject from being merely exercise.

In discussing metabolic patterns the authors indulge in the common and accepted practice of using abbreviations for names of compounds and systems. Although the reason for such practice is obvious, it could be confusing to the uninitiated. Because of the audience for which the book is intended, it is suggested that the page of nomenclature which precedes the text be extended to include all the abbreviations used. It is doubtful that on page 271 the general reader will recognize TPP as thiamine pyrophosphate as explained in the previous chapter on page 261.

The charts and tables are numerous and clear and should add to the usefulness of the book. The authors are to be commended for including an excellent introduction to energetics. Until recently energy relationships have been neglected by biochemistry texts and general discussions of enzymatic reactions, yet it is the subject about which many botanists and physiologists are asking questions of their biochemist friends. This book is enjoyable reading and is well recommended.—FRANCIS L. ESTES, Department of Chemistry, Douglass College, Rutgers University.

Speciation and Variation in Asexual Fungi. By K. B. Raper (Chairman), L. Anderson, E. J. Backus, M. P. Backus, R. G. Benedict, R. E. Buchanan, P. R. Burkholder, T. H. Campbell, A. Dietz, B. M. Duggar, E. L. Dulaney, J. Ehrlich, H. N. Hansen, C. W. Hesseltine, K. L. Jones, D. M. MacLeod, N. M. McClung, W. J. Nickerson, T. G. Pridham, W. C. Snyder, J. F. Stauffer, S. H. Sun and C. Thom. Published as Annals of the New York Academy of Sciences **60** (Art. 1): 1–182. 1954.

The participants in this symposium on "Speciation and Variation in Fungi" pointed out that because they were dealing with non-sexual forms it was necessary for investigators to determine what characters were most suitable for species delimitation. Elimination of highly variable characters should leave those that are suitable for use.

That variation among single-spore isolates of a culture may give rise to noticeable differences was discussed in *Fusarium*, *Beauveria* and actinomycetes. Variation among natural isolates that appear to be one species was discussed for *Fusarium*, *Beauveria* and other entomogenous fungi and especially in several species of *Streptomyces*. Variation due to nutritional factors was repeatedly observed in nearly all fungi under consideration. The effect of mutagenic treatments in giving rise to variants was an important part of papers dealing with *Penicillium chrysogenum*, *Streptomyces aureofaciens*, and *S. griseus*.

Methods of study of bacteria, actinomycetes and some other fungi were outlined and evaluated. Especially for the genus *Streptomyces* was there noteworthy elaboration of methods and media and comments on the problems of speciation.

If the viewpoint expressed in these papers prevails, we may expect to see more and more specific names in lists of synonyms and to find the concept of "species aggregate"

being used more frequently in efforts to make workable and satisfactory disposition of fungal cultures of certain genera.

This well-illustrated series of papers summarizes nicely much of our present knowledge about methods of studying certain fungi and is a useful addition to our literature. —JOHN B. ROUTIEN, Department of Biochemical Research, Chas. Pfizer and Co., Inc., Brooklyn 6, New York.

Auxins and Plant Growth. By A. Carl Leopold. University of California Press, Berkeley 4, California. pp. vii + 354. 1955. $5.00.

One of the largest gaps in the chain of knowledge linking pure and applied science is the failure of the pure research worker to make available the basic concepts implicit in his work in a form understandable to the technical worker. This is true in plant physiology and plant biochemistry where research reports are accumulating at a rate beyond the capacity of any worker even to stay abreast of his own specialty, much less in related but equally germane branches of the science. In areas of research, well illustrated by the auxins, where technical applications of research findings are often made before the ink is completely dry on the journal page, the problem is very acute. It is here that Dr. Leopold has attempted, with considerable success, to put together the pertinent findings and give the technologist the necessary background to use intelligently the plethora of information available to him.

This book is divided into two main sections, the first being an abbreviated course in the physiology and biochemistry of auxins, the second dealing with the agricultural and horticultural applications of the basic findings. This procedure permits the technical worker to grasp the fundamental rationale upon which, to be successful, all technical applications must be based. The first section is not, however, sufficiently detailed or documented to supplant the chapters available in the Annual Reviews and is, therefore, not suitable for advanced research workers in plant physiology. An important criticism is the failure of the author to differentiate between known facts and postulates for which proof is still lacking. This is particularly noticeable in those chapters dealing with the mechanisms of auxin action and the effects of auxins on development. This does not seriously detract from the value of the volume for the applied scientist.

The organization of the sections on pure and applied aspects is parallel throughout the book and is well integrated. The figures are clear, well made and all of them compliment the well-printed, readable text. An adequate bibliography and index are included. The book will be of considerable utility to workers in applied agriculture and horticulture.—RICHARD M. KLEIN, New York Botanical Garden.

NOTE

The purchase of **Mettler's Woods** has been completed by a memorial grant from the United Brotherhood of Carpenters and Joiners of America. A ceremony of dedication and title change will be held at the Woods and at Rutgers University on October 15, 1955. The Torrey Botanical Club is invited to participate.

The Appalachian Trail work trip of April 24 was rained out before completing its tasks. The Trail in our section is easily travelled and we shall return to complete clearing and painting blazes on October 22, Saturday. Bring your tools and enjoy the autumn color of Kittatinny Ridge. Meet at Blairstown post office at 10:00.—J. A. S.

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INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

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